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WHEAT AND WHEAT IMPROVEMENT

Second Edition

AGRONOMY

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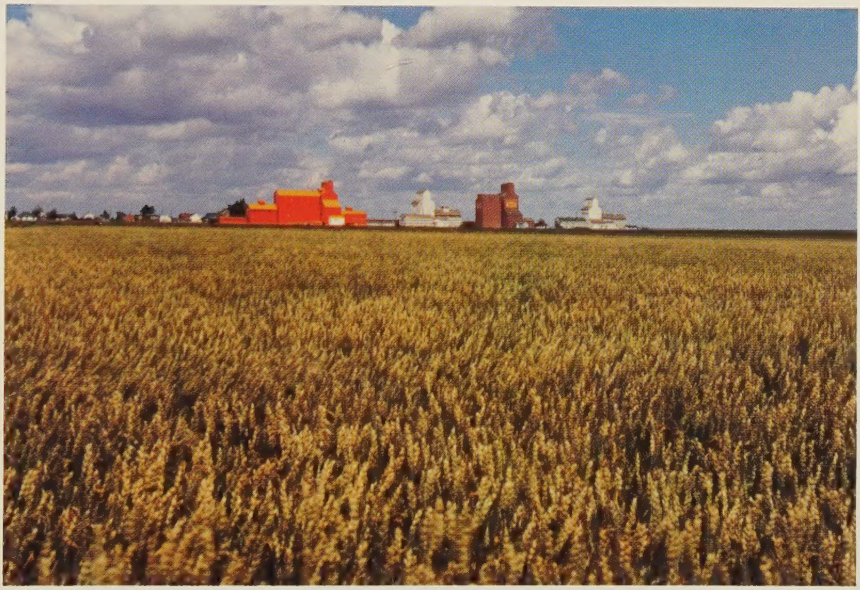

Mature wheat (*top*) and wheat field and elevators (*bottom*) in the Northern Great Plains. Courtesy, Dr. H. M. Austenson, University of Saskatchewon, Saskatoon, Canada.

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FOREWORD

The American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America are pleased to present this volume, a revision of Agronomy Monograph 13, *Wheat and Wheat Improvement*, first published in 1967. Although some of the topics of this volume were in the earlier monograph, all chapter authors are different and all chapters of this revision are original with the current authors.

This volume includes recent advances in our knowledge of wheat as well as important information contained in the original monograph. The American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America acknowledge the significant service of the authors and reviewers who have volunteered their time, skill, and knowledge to bring this monograph to you.

Dale N. Moss, *president*, 1986
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PREFACE

The first edition of *Wheat and Wheat Improvement* was published in 1967. It has been reprinted once. Although many facts and information in the first edition are still useful, there has been an accumulation of published material which justifies updating the original monograph. Even in the field of anatomy and morphology more than 80% of the references cited have been published since 1967.

Major advances have occurred in the fields of biochemical research, molecular genetics, chromosomal banding, hybrid wheat, breeding techniques, pathology and insect and disease control, an understanding of physiological functions, production management, and refined techniques in evaluating quality. New developments in these areas are discussed in this monograph.

Wheat still remains the major cereal crop source for our food. This has been so since the first domestication of plants and animals more than 10 000 years ago. Wheat will no doubt remain a primary food source because of its adaptation throughout the world and its successful production in marginal agricultural areas.

In November 1981, Sterling R. Olson, president of ASA, appointed the present editorial committee to proceed with the revision of the Wheat monograph. The format is similar to the first edition except that the topics of "Experimental Milling" and "Marketing Wheat" are not included in the second edition.

The editorial committee wishes to express its appreciation to the 46 authors from Australia and North America who made this publication possible. Thanks also are due to those who reviewed various sections and chapters. The reviewers were: R. E. Allan, R. J. Baker, T. Burnouf, A. Ciha, J. R. Crabtree, J. Dvorak, M. D. Gale, R. J. Hanks, R. C. Johnson, D. D. Kasarda, E. L. Klepper, B.D.H. Latter, A. McHughen, D. S. Murphy, F. Patterson, G. M. Paulsen, W. F. Pfender, J. S. Quick, J. W. Schmidt, G. J. Scoles, E. R. Sears, B. A. Stewart, J. F. Stone, S. D. Tanksley, D. The, T. C. Todd, R. L. Westerman, and W. G. Willis.

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Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Unit	To convert Column 2 into Column 1 multiply by
	Length		
0.621	kilometer, km (10^3 m)	mile, mi	1.609
1.094	meter, m	yard, yd	0.914
3.28	meter, m	foot, ft	0.304
1.0	micrometer, μm (10^{-6} m)	micron, μ	1.0
3.94×10^{-2}	millimeter, mm (10^{-3} m)	inch, in	25.4
10	nanometer, nm (10^{-9} m)	Angstrom, Å	0.1
	Area		
2.47	hectare, ha	acre	0.405
247	square kilometer, km^2 (10^3 m)^2	acre	4.05×10^{-3}
0.386	square kilometer, km^2 (10^3 m)^2	square mile, mi^2	2.590
2.47×10^{-4}	square meter, m^2	acre	4.05×10^3
10.76	square meter, m^2	square foot, ft^2	9.29×10^{-2}
1.55×10^{-3}	square millimeter, mm^2 (10^{-6} m)^2	square inch, in^2	645
	Volume		
6.10×10^4	cubic meter, m^3	cubic inch, in^3	1.64×10^{-5}
2.84×10^{-2}	liter, L (10^{-3} m^3)	bushel, bu	35.24
1.057	liter, L (10^{-3} m^3)	quart (liquid), qt	0.946
3.53×10^{-2}	liter, L (10^{-3} m^3)	cubic foot, ft^3	28.3
0.265	liter, L (10^{-3} m^3)	gallon	3.78
33.78	liter, L (10^{-3} m^3)	ounce (fluid), oz	2.96×10^{-2}
2.11	liter, L (10^{-3} m^3)	pint (fluid), pt	0.473
9.73×10^{-3}	$meter^3$, m^3	acre-inch	102.8
35.3	$meter^3$, m^3	cubic foot, ft^3	2.83×10^{-2}

continued on next page

Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Unit	To convert Column 2 into Column 1 multiply by
	Mass		
2.20×10^{-3}	gram, g (10^{-3} kg)	pound, lb	454
3.52×10^{-2}	gram, g	ounce (avdp), oz	28.4
2.205	kilogram, kg	pound, lb	0.454
10^{-2}	kilogram, kg	quintal (metric), q	10^{2}
1.10×10^{-3}	kilogram, kg	ton (2000 lb), ton	907
1.102	megagram, Mg (tonne)	ton (U.S.), ton	0.907
	Yield and Rate		
0.893	kilogram per hectare, kg ha^{-1}	pound per acre, lb $acre^{-1}$	1.12
7.77×10^{-2}	kilogram per cubic meter, kg m^{-3}	pound per bushel, lb bu^{-1}	12.87
1.49×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 60 lb	67.19
1.59×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 56 lb	62.71
1.86×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 48 lb	53.75
0.107	liter per hectare, L ha^{-1}	gallon per acre	9.35
893	megagram per hectare, Mg ha^{-1}	pound per acre, lb $acre^{-1}$	1.12×10^{-3}
0.446	megagram per hectare, Mg ha^{-1}	ton (2000 lb) per acre, ton $acre^{-1}$	2.24
2.24	meter per second, m s^{-1}	mile per hour	0.447
	Specific Surface		
10	square meter per kilogram, m^2 kg^{-1}	square centimeter per gram, cm^2 g^{-1}	0.1
10^{3}	square meter per kilogram, m^2 kg^{-1}	square millimeter per gram, mm^2 g^{-1}	10^{-3}

Pressure

9.90	megapascal, MPa (10^6 Pa)	atmosphere	0.101
10	megapascal, MPa (10^6 Pa)	bar	0.1
1.00	megagram per cubic meter, Mg m^{-3}	gram per cubic centimeter, g cm^{-3}	1.00
2.09×10^{-2}	pascal, Pa	pound per square foot, lb ft^{-2}	47.9
1.45×10^{-4}	pascal, Pa	pound per square inch, lb in^{-2}	6.90×10^3

Temperature

1.00 (K − 273)	Kelvin, K	Celsius, °C	1.00 (°C + 273)
(9/5 °C) + 32	Celsius, °C	Fahrenheit, °F	5/9 (°F −32)

Energy, Work, Quantity of Heat

9.52×10^{-4}	joule, J	British thermal unit, Btu	1.05×10^3
0.239	joule, J	calorie, cal	4.19
10^7	joule, J	erg	10^{-7}
0.735	joule, J	foot-pound	1.36
2.387×10^{-5}	joule per square meter, J m^{-2}	calorie per square centimeter (langley)	4.19×10^4
10^5	newton, N	dyne	10^{-5}
1.43×10^{-3}	watt per square meter, W m^{-2}	calorie per square centimeter minute (irradiance), cal cm^{-2} min^{-1}	698

Transpiration and Photosynthesis

3.60×10^{-2}	milligram per square meter second, mg m^{-2} s^{-1}	gram per square decimeter hour, g dm^{-2} h^{-1}	27.8
5.56×10^{-3}	milligram (H_2O) per square meter second, mg m^{-2} s^{-1}	micromole (H_2O) per square centimeter second, μmol cm^{-2} s^{-1}	180
10^{-4}	milligram per square meter second, mg m^{-2} s^{-1}	milligram per square centimeter second, mg cm^{-2} s^{-1}	10^4
35.97	milligram per square meter second, mg m^{-2} s^{-1}	milligram per square decimeter hour, mg dm^{-2} h^{-1}	2.78×10^{-2}

continued on next page

Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Unit	To convert Column 2 into Column 1 multiply by
		Angle	
57.3	radian, rad	degrees (angle), °	1.75×10^{-2}
		Electrical Conductivity	
10	siemen per meter, S m^{-1}	millimho per centimeter, mmho cm^{-1}	0.1
		Water Measurement	
9.73×10^{-3}	cubic meter, m^3	acre-inches, acre-in	102.8
9.81×10^{-3}	cubic meter per hour, $m^3\ h^{-1}$	cubic feet per second, $ft^3\ s^{-1}$	101.9
4.40	cubic meter per hour, $m^3\ h^{-1}$	U.S. gallons per minute, gal min^{-1}	0.227
8.11	hectare-meters, ha-m	acre-feet, acre-ft	0.123
97.28	hectare-meters, ha-m	acre-inches, acre-in	1.03×10^{-2}
8.1×10^{-2}	hectare-centimeters, ha-cm	acre-feet, acre-ft	12.33
		Concentrations	
1	centimole per kilogram, cmol kg^{-1} (ion exchange capacity)	milliequivalents per 100 grams, meq 100 g^{-1}	1
0.1	gram per kilogram, g kg^{-1}	percent, %	10
1	megagram per cubic meter, Mg m^{-3}	gram per cubic centimeter, g cm^{-3}	1
1	milligram per kilogram, mg kg^{-1}	parts per million, ppm	1
		Plant Nutrient Conversion	
	Elemental	***Oxide***	
2.29	P	P_2O_5	0.437
1.20	K	K_2O	0.830
1.39	Ca	CaO	0.715
1.66	Mg	MgO	0.602

1 Wheat Worldwide

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Common wheat (*Triticum aestivum* L. em. Thell.) is grown across a wide range of environments around the world; in fact, it has the broadest adaptation of all the cereal crop species. More land is devoted worldwide to the production of wheat than to any other commercial crop. Wheat is the number one food grain consumed directly by humans, and its production leads all crops, including rice, maize, and potatoes.

Wheat is a cool-season crop, but it flourishes in many different agroclimatic zones. Production is concentrated between latitudes 30 and 60°N and 27 and 40°S (Nuttonson, 1955; Percival, 1921) (Fig. 1–1). However, wheat can be and is grown beyond these limits. For example, in the Northern Hemisphere, wheat can be grown from within the Artic Circle to the equator, if, in the latter case, it is cultivated at locations of sufficiently high elevation.

The minimum temperature for growth is about 3 to 4°C, the optimum temperature is about 25°C, and the maximum is about 30 to 32°C (Briggle, 1980). Wheat grows best on well-drained soils from sea level to about 3000 m above sea level (masl). In some tropical countries, wheat is being grown from 2000 to 3200 masl, and it has been reported at 4270 to 4570 masl in Tibet (Percival, 1921). The species can be grown in most locations where annual precipitation ranges from 250 to 1750 mm; about three-fourths of the land area used for wheat production receives an average of between 375 and 875 mm annually (Leonard and Martín, 1963). While wheat can be grown on residual moisture alone in some areas (such as in northern Thailand), the seasonal distribution of precipitation is a critical factor in most production environments.

A crop of wheat is harvested somewhere in the world during every month of the year (Briggle, 1980; Percival, 1921). Most of the global harvest, however, occurs between April and September in the temperate

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Wheat and Wheat Improvement—Agronomy Monograph no. 13. (2nd Edition).

Fig. 1–1. Major areas of wheat production around the world. Source: Goode's World Atlas, 1975; updated by CIMMYT, 1984.

zone of the Northern Hemisphere; considerably less wheat is grown in the Southern Hemisphere where harvest occurs from October to January.

Wheat has unique baking properties, the most important of which is the elasticity of its gluten. The amount and quality of the gluten produced by any particular genotype are prime factors in determining the quality of the flour that can be obtained from the milling process (Bushuk and Wrigley, 1974). Unlike any other grain or plant product, wheat gluten enables dough to rise through the formation of minute gas cells that retain the carbon dioxide formed during yeast fermentation or chemical leavening (Briggle, 1980; Bushuk and Wrigley, 1974; Cotton and Ponte, 1974; Inglett, 1974). This special property of wheat gluten allows the baking of leavened bread, a practice that is believed to have originated in Egypt (Briggle, 1980; Häfliger, 1980). Bread, both leavened and unleavened, has been a basic food for man throughout recorded history, and probably for a much longer period; it remains the principal food product made from wheat.

On a global basis, wheat provides more nourishment for people than any other food source (Johnson et al., 1978; Reitz, 1967), and is the most important source of carbohydrates in the majority of countries in the temperate zone (Leonard and Martín, 1963). Wheat is an excellent food, even though the grain is deficient in some essential amino acids (it is particularly low in lysine). Wheat starch is easily digested, as is most wheat protein. The grain contains minerals, vitamins, and fats (lipids), and when wheat products are complemented by small amounts of animal or legume protein, the combination is highly nutritious (Johnson et al., 1978; Reitz, 1967). A predominantly wheat-based diet is higher in fiber and lower in fats than a meat-based diet.

A significant amount of wheat also is used for animal feed. The actual amount varies from year to year, depending almost entirely on the price of wheat in relation to maize (*Zea mays* L.) and other feed grains. In general, and on a kilogram-for-kilogram basis, wheat is about equal to maize, barley (*Hordeum vulgare* L.), or steam-flaked sorghum [*Sorghum bicolor* (L.) Moench] when used in high-concentrate beef (*Bos taurus*)-fattening rations, as long as a minimum of 5% roughage is included (Saunders et al., 1974). Wheat is usually fed in combination with one or more other feed grains. It is an acceptable swine (*Sus scrofa domesticus*) feed, but is not as efficient as maize for that purpose. Wheat makes an excellent poultry feed. After milling, about 25% of the whole grain weight ends up as secondary fractions (bran, germ, shorts) and most of these by-products are used to good advantage by the feed manufacturing industry.

Small amounts of wheat and wheat flour are used by various industries. Wheat starch is similar to maize, potato (*Solanum tuberosum* L.), and other starches, which are less expensive. The wheat starch used in industry is derived from low-grade or damaged wheat, or from the least desirable flour fractions after milling. Wheat starch is used for laundering, paper laminating and corrugating, adhesives, textiles, wallpaper and billboard paste, and paper additives (Miller, 1974). Low-grade wheat also is

fermented for the production of alcohol. Gluten, when separated from other flour components, can be used very effectively to increase the total protein in baked goods and other food products, to improve low protein flours, as a texturizing protein and meat substitute in all-vegetable meat-like products, and as a meat or fish extender.

1–1 WORLD PRODUCTION AND COMMERCE

Between 1960 and 1985 world wheat production increased dramatically, while the total area harvested has increased only slightly (USDA, 1985) (Fig. 1–2). A record amount of wheat, 514.5 Tg, was produced during the 1984–1985 crop year. This constitutes a doubling of annual production during the 25-yr period.

From 1971 to 1981, wheat production increased proportionately more in developing countries than in developed countries (nearly a 50% increase, compared to 35%) (CIMMYT, 1983; Curtis, 1982). However, in absolute terms (Tg) slightly more than half of the total increase in global production occurred in the developed world.

1–1.1 Yields and Yield Dependability

By far, most of this increase in global production resulted from higher yields, a conclusion supported by a comparison of Fig. 1–2 and 1–3. The

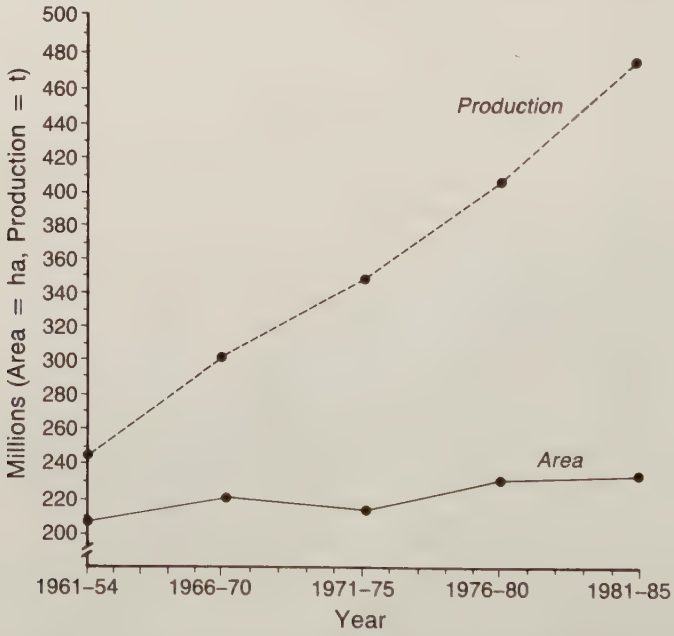

Fig. 1–2. Wheat area harvested and tonnes of grain produced worldwide. Source: USDA wheat outlook and situation report, WS 273, September 1985. Foreign agricultural circular, FG-6-84, March 1984.

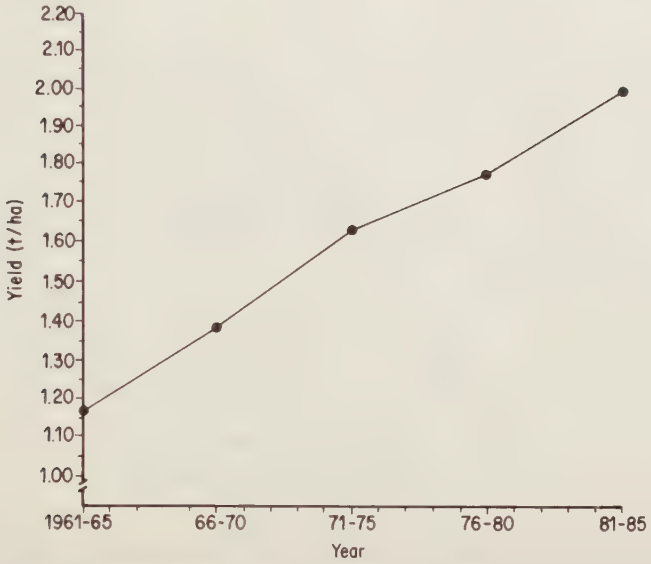

Fig. 1–3. Wheat yields: tonnes produced per hectare worldwide (1984–1985 data are projected).

yield curve shown in Fig. 1–3 is practically identical in shape to the total production curve displayed in Fig. 1–2. While it is not possible to determine accurately how much of the increase in yield can be attributed to the greater genetic yield potential of improved cultivars and how much can be attributed to better cultural and management practices, the genetic contribution has been significant. The widespread adoption of improved, high-yielding, semidwarf wheat cultivars (often referred to in the literature as HYVs) in many developing countries has greatly increased the global genetic potential for higher yields (Dalrymple, 1986).

Moreover, recent evidence indicates that use of the management-responsive semidwarf wheats has substantially increased the dependability of wheat yields in the developing world (Pfeiffer, 1983). (Yield dependability refers to the consistency of yield across time and environments.) Certain of the semidwarf cultivars perform better than locally developed cultivars across all environments, even under stress. An example is the cv. Veery developed by the International Maize and Wheat Improvement Center in Mexico (CIMMYT) (now released as 'Pak 81' in Pakistan), which can be classified as a universal cultivar (Fig. 1–4). It usually yields higher than other cultivars in spring wheat environments, probably because of its more efficient utilization of available inputs and its broad-based resistance to prevalent diseases, which can make an otherwise fertile environment a low-yielding one (Curtis, 1982).

The more widespread use of production inputs also appears to have played a part in enhancing the dependability of yield. During the period in which the new semidwarf cultivars were rapidly replacing traditional types, there was a dramatic increase in the use of certain inputs, primarily

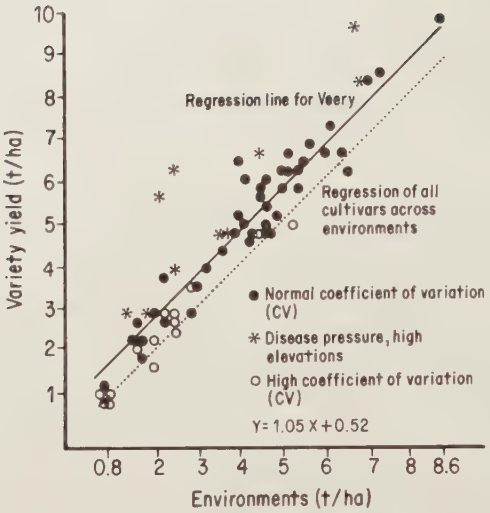
Variety yield (t/ha)
Environments (t/ha)
Regression line for Veery
Regression of all cultivars across environments
Normal coefficient of variation (CV)
Disease pressure, high elevations
High coefficient of variation (CV)
Y = 1.05 X + 0.52

Fig. 1–4. Response of the CIMMYT cv. Veery (Pak 81) to varying environments. Source: Pfeiffer (1983).

N fertilizer and irrigation water. In 1974 the global use of N fertilizer was about 40 Tg. In 1981, only 7 yr later, the amount had increased to about 50 Tg, a rise of 25% (Curtis, 1982). The greater use of fertilizer, coupled with a significant increase in irrigation in some areas (and water-conserving cultural practices in drier locations), contributed significantly to yield increases.

1–1.2 The Leading Producers

Most of the world's wheat-producing countries as of 1982 are listed in Table 1–1. At that time, the USSR devoted more land to growing wheat than any other country, and was the world's leading producer. The USA and the People's Republic of China (PRC) ranked second and third, respectively; these two countries differed little from one another in the amount of land planted to wheat and in total production. Dramatic changes have occurred since 1982. In 1984 the PRC became the world's leading wheat producer (USDA, 1985), and the European Community (EC-10: Belgium, Denmark, France, Federal Republic of Germany, Greece, Ireland, Italy, Luxembourg, Netherlands, and United Kingdom) advanced to second place. USDA projections for 1985 list 87.0 Tg for PRC, 83.0 Tg for the USSR, 70.1 Tg for the EC-10, and 64.7 Tg for the USA. India, France, Turkey, and Pakistan markedly increased their production of wheat after the early 1960s. India's 1984 wheat crop set a new record of 45.1 Tg and, based on production figures averaged from 1980 to 1985, India produces considerably more wheat than the exporting countries of Canada, Australia, and Argentina. It is interesting to note that most of the leading wheat-producing countries have rather limited yields per hec-

Table 1–1. Selected wheat statistics for specified countries, 1979–1982, from *FAO Trade and Production Yearbooks.*

Country	Area	Yield	Production	Net imports†		Production	Consumption‡
	1 000 ha	Mg ha⁻¹	1 000 Mg	1 000 Mg	kg per capita	kg per capita	
North America							
USA	29 687	2.3	68 852	(39 556)	(173)	301	128
Canada	11 678	1.9	22 020	(16 493)	(681)	909	228
Mexico	803	4.0	3 179	865	12	45	57
Guatemala	44	1.2	55	105	14	7	22
South America							
Bolivia	100	0.7	65	305	54	12	66
Peru	88	1.1	100	815	46	6	51
Colombia	38	1.5	55	470	18	2	20
Ecuador	32	1.1	36	245	30	4	34
Argentina	5 883	1.7	9 828	(4 132)	(152)	361	209
Brazil	2 925	0.8	2 422	4 250	34	20	54
Chile	478	1.7	824	928	83	74	156
Uruguay	269	1.3	360	(3)	(1)	123	122
Paraguay	55	1.1	58	61	19	18	37
Western Europe							
France	4 568	5.0	22 857	(11 371)	(211)	425	213
Italy	3 361	2.7	8 967	1 723	30	157	187
Spain	2 637	1.7	4 490	(210)	(6)	120	115
Germany, Fed. Rep. of	1 626	5.1	8 291	(132)	(2)	135	133
United Kingdom	1 491	5.8	8 666	711	13	154	167
Greece	983	2.8	2 773	(776)	(80)	287	206
Belgium/Luxembourg	188	5.2	979	321	31	96	127
Netherlands	136	6.5	892	685	48	63	111

(continued on next page)

Table 1–1. Continued

Country	Area	Yield	Production	Net imports†		Production	Consumption‡
	1 000 ha	Mg ha^{-1}	1 000 Mg	1 000 Mg	kg per capita	kg per capita	
Eastern Europe							
Romania	2 154	2.7	5 718	399	18	257	275
Poland	1 508	2.8	4 261	3·400	95	119	214
Yugoslavia	1 496	3.2	4 773	737	33	213	246
Hungary	1 218	4.1	5 041	(937)	(88)	471	383
Czechoslovakia	1 108	4.1	4 513	394	26	295	312
Bulgaria	1 004	4.1	4 139	(448)	(51)	466	416
German Dem. Rep.	671	4.4	2 974	591	35	178	213
USSR	58 917	1.5	88 870	14 273	54	333	387
East Asia							
China	28 676	2.1	61 503	12 348	12	61	74
Mongolia	418	0.7	291	107	63	172	235
Japan	198	3.1	613	5 581	48	5	53
Korea, D.P.R. of	159	2.5	403	571	32	22	54
Korea, Rep. of	20	3.2	64	1 886	49	2	50
South Asia							
India	22 309	1.6	32 276	990	1	51	53
Pakistan	6 954	1.6	10 896	877	10	124	134
Bangladesh	456	1.9	844	1 135	13	9	22
Nepal	379	1.2	465	9	1	32	33
Middle East							
Turkey	9 144	1.9	17 166	(366)	(8)	375	367
Iran	5 901	1.1	6 241	1 197	31	161	192
Afghanistan	2 247	1.2	2 781	76	5	172	177
Syria	1 343	1.3	1 800	328	36	197	232

(continued on next page)

Table 1–1. Continued

Country	Area	Yield	Production	Net imports†		Production	Consumption‡
Iraq	1 203	0.7	882	1 760	132	66	199
Jordan	108	0.6	63	338	102	19	121
Israel	94	2.0	187	499	128	48	176
Saudi Arabia	92	2.3	214	767	84	23	107
North Africa							
Algeria	1 985	0.6	1 217	2 695	140	63	203
Morocco	1 676	1.0	1 671	1 798	87	81	168
Tunisia	844	1.0	857	626	97	133	231
Egypt	577	3.3	1 904	5 428	128	45	173
Libya	264	0.5	133	535	176	44	220
East and East Central Africa							
Ethiopia	599	1.2	690	258	8	22	30
Sudan	193	1.0	195	324	17	11	28
Kenya	108	2.1	222	65	4	13	17
Tanzania	57	1.4	79	55	3	4	7
Zimbabwe	36	5.1	184	1	0	24	25
Lesotho	27	0.9	23	66	49	17	66
South Africa							
South Africa, Union of	1 820	1.1	2 079	39	1	70	71
Oceania							
Australia	11 467	1.1	13 071	(10 890)	(747)	897	150
New Zealand	83	3.8	312	34	11	100	111

†Numbers in parentheses refer to exports.

‡Consumption is based on production plus imports minus exports divided by population number. These figures do not take into account stocks that may have been on hand.

tare (Table 1–1), with the exception of some countries in northwestern Europe where yields often average more than 5 Mg ha^{-1}. During 1983 and 1984, England achieved average yields of more than 6 Mg ha^{-1}.

1–1.3 Exports and Imports

Most wheat is used entirely within the country in which it is produced (Briggle, 1980; Reitz, 1967); very few countries produce in excess of their own needs. By a wide margin, the USA is the leading wheat-exporting country (Table 1–1). In recent years, about two-thirds of the USA's wheat production entered the export market. One explanation for the USA's leadership in exporting wheat is the wide range of both hard and soft wheats produced. Even kernel color varies within important classes of wheat. There also is a wide range in grain protein (from 7 to 8% in soft wheats to as high as 19 to 20% in hard wheats) (Johnson et al., 1978).

The USSR was once an important exporter of wheat, but since 1975 its exports have been minor and destined primarily for neighboring eastern European countries. The USSR is now the world's leading wheat importer (Table 1–1), even though it still produces more than most other nations.

Both Canada and Australia export about three-fourths of their annual production (Woodhams, 1980). Canada has long been an important source of high quality, high protein wheat for importing countries. Australia supplies a range of hard, semihard, and soft white wheats, but production fluctuates considerably from year to year.

European Community (EC-10) exports have increased in recent years, primarily because of increased production in France and England; a large part of EC-10 exports are in the form of flour (Woodhams, 1980). Argentina is the only developing country that is an important wheat exporter (an average of 4.3 Tg during the years 1979 to 1982) (Table 1–1).

A considerable expansion in world wheat trade occurred since the early 1970s. From 1970 to 1983, trade grew from about 53 Tg to an estimated 101 Tg per year, and in 1981–1982 developing countries as a group imported 62 Tg of wheat (Curtis, 1982). Most of the expansion in world wheat trade is due to increased imports by developing countries. In fact, wheat enters into international trade more than any other food crop (Johnson et al., 1978).

1–1.4 Consumption Patterns

The consumption of wheat products worldwide is changing (Curtis, 1982). Since the early 1970s, the average annual rate of wheat consumption in the developed countries of the world has leveled off at about 175 kg per capita. In developing countries, however, wheat is now an important source of calories and, to a lesser extent, protein in the diet of

millions of people. The consumption of wheat by these people increased by about 73% from 1972 to 1982. This trend shows no signs of abating (CIMMYT, 1983).

One reason for the explosive increase in Third World wheat consumption is a shift in basic tastes and preferences; wheat is increasingly preferred instead of rice (*Oryza sativa* L.) and such coarse grains as maize and sorghum. During the period 1963 to 1976, for example, the per capita direct human consumption of wheat in all developing countries rose by about 35%; the increase for rice was 6%, maize showed no increase, and the direct per capita consumption of millets (*Setaria, Panicum* and *Pennisetum* spp.), sorghum, roots (turnips, *Brassica* Spp.), and tubers (potatoes and sweet potatoes, *Ipomoea batata*) declined by 14 to 15% (Curtis, 1982). About 20% of all wheat exports are now going to the more tropical countries of such regions as Sub-Saharan Africa, Southeast Asia, and Latin America. Wheat is not a traditional crop in most of these countries, and little, if any, is currently produced there.

Demographic shifts and changing income levels are affecting wheat consumption patterns in developing countries (CIMMYT, 1983; Curtis, 1982). Recent surveys indicate that wheat consumption is much higher in urban than in rural areas and by middle and upper income groups. Urbanization is occurring at a rapid rate and in most of these countries income levels are rising. This signals a continuation of the trend toward higher levels of wheat consumption in the developing world.

Rapid increases in wheat consumption outpaced domestic production in many Third World countries, even though some of them significantly expanded their output (Woodhams, 1980). Food aid from developed countries, much of it in the form of wheat or wheat flour, has certainly encouraged wheat consumption by developing countries (CIMMYT, 1983; Woodhams, 1980). Both the promotion of wheat as the basic component in food-aid programs and the provision of technical assistance and training to help establish domestic wheat product industries in developing countries have stimulated wheat consumption in the Third World.

The growing importance of developing countries in providing markets for burgeoning world wheat supplies is a principal element in the international wheat situation (CIMMYT, 1983; Woodhams, 1980). Another element is the considerable variability that exists in year-to-year global production, which is caused primarily by fluctuating yields. Most wheat is grown in marginal agroclimatic zones where output can be affected by drought, excessive moisture (particularly at planting and/or harvest), high or low temperatures, and diseases and/or pests. Like production, trade also fluctuates from year to year, with some countries making large purchases in certain years because of wheat crop disasters or because of changes in foreign policy.

1–2 WHEAT AROUND THE WORLD

1–2.1 North America

1–2.1.1 USA.

Wheat is second only to maize in the USA in terms of area planted and production. Five classes of wheat are grown (Table 1–2) in four regions (Fig. 1–5) Most U.S. wheat is grown in the Plains states, from Texas in the south to North Dakota in the north. The total area planted each year is highly influenced by the government's price support and agricultural land control programs (such as the 1983 Payment In Kind [PIK] program). In 1981, the USA harvested 32 785 150 ha of wheat, a record for the country that still stood as of this writing (1985). The highest level of production occurred in 1982, when 76 443 000 Mg were produced (CIMMYT, 1983). Only about 5% of the USA wheat area was irrigated in 1974 (U.S. Department of Commerce, 1978).

Five principal classes of wheat are grown: hard red winter (HRW), hard red spring (HRS), soft red winter (SRW), white, and durum (Table 1–2). Most HRW wheat is grown in the central and southern Plains states; most HRS wheat is grown in the northern Plains states; and essentially all SRW is grown in the East. White wheat, both winter and spring habit, is grown in the Pacific Northwest, and white winter wheat in two eastern states, Michigan and New York; most durum wheat is grown in the northern Great Plains, primarily in North Dakota.

Nearly half of the total U.S. wheat production is of the HRW class (Table 1–2). During the past 5 yrs, an increasing area has been planted to SRW wheat. In states like Illinois and Missouri, there has been a shift from about 50% HRW to more than 90% SRW wheat. A dramatic increase of SRW wheat also has occurred in the southeastern states, particularly in Alabama, Arkansas, Georgia, Louisiana, Mississippi, South Carolina, and Tennessee. Nearly all of this increase resulted from greater cropping intensity, e.g., the double-cropping of wheat with soybean [*Glycine max* (L.) Merr.]. Food products made from the different classes of U.S. wheat, whether for domestic use or for export, are listed in Table 1–3.

The predominant cultivars planted change frequently because of constant improvements in disease and insect resistance, productivity, straw characteristics, maturity, and response to management. Of the 429 cultivars planted in the USA in 1984, 19 accounted for half the total area planted. North American farmers are eager to take advantage of new technology, whether in the form of improved cultivars, new management techniques, more efficient equipment, or more effective fertilizers, herbicides, insecticides, and fungicides. All these factors have improved the stability of U.S. wheat production (Reitz, 1967).

A change is taking place in the pattern of cultivar development and release in the USA. In 1979, 89.8% of the total wheat area planted was in cultivars developed and released by public agencies (Briggle et al.,

Table 1–2. Classes of wheat produced in the USA.

Class	Region grown	Production and percentage of total		
		1981	1982	1983
		Mg		
Hard red winter	Great Plains Winter Wheat Region	30 390 601 (39.9)	34 166 443 (44.6)	32 473 918 (49.2)
Hard red spring	Great Plains Spring Wheat Region	12 729 547 (16.7)	13 612 592 (17.8)	8 509 680 (12.9)
Soft red winter	Eastern Wheat Region	18 410 605 (24.2)	16 693 504 (21.8)	13 924 893 (21.1)
White	Western and Eastern Wheat Regions	9 578 690 (12.6)	8 052 018 (10.5)	9 114 796 (13.8)
Durum	Great Plains Spring Wheat Region (minor amount in Western Wheat Region)	5 060 510 (6.6)	4 014 415 (5.2)	1 986 183 (3.0)
All wheat	USA	76 169 953	76 538 972	66 009 470

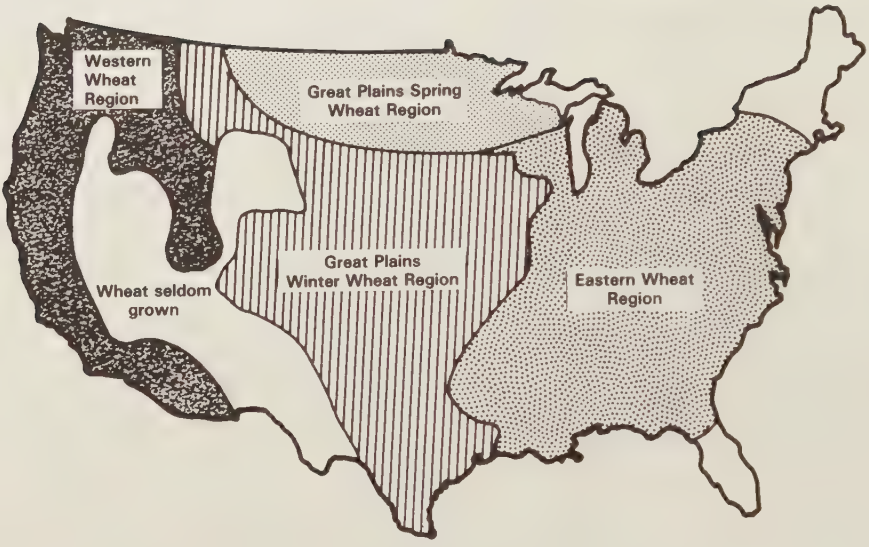

Fig. 1–5. Wheat-growing regions of the USA.

Table 1–3. Food products made from different classes of wheat.

Species		
Triticum aestivum and *T. compactum*		*T. durum*
Classes		
Hard red winter	Soft red winter	Durum
Hard red spring	Soft white winter	
Hard white winter	Soft white spring	
Hard white spring		
Products		
Bread	Crackers	Macaroni
Rolls	Cookies	Spaghetti
Chapatis	Cakes	Puffed breakfast cereals
Bagels	Biscuits	Egg noodles
English muffins	Donuts (cake)	Wheat germ
Sweet goods	Pancakes	
Hot breakfast cereals	Waffles	
Farina	Muffins	
Wheat germ	Oriental noodles	
Pita or flat style breads	Pie crust	
Donuts (yeast raised)	Bulgur	
Pizza	Ice cream cones	
Puff pastry	Flaked breakfast cereals	
Puffed breakfast cereals	Puffed breakfast cereals	
	"Natural" breakfast cereals	
	Baby foods	
	Puff pastry	
	Soup thickeners	
	Gravy thickeners	
	Sauce thickeners	
	Wheat germ	
	Pita or flat style breads	

1982). In 1984, the percentage had dropped to 81.3 (Siegenthaler et al., 1986). Two major events, the potential for making wheat hybrids on a field scale and the Plant Variety Protection Act (7 U.S.C. 2321 et seq.), are responsible for the significantly increased involvement of private industry in cultivar development. In the early 1960s, cytoplasmic male sterility and fertility-restoring genes were found in wheat. These made possible the production of hybrid wheat on a commercial scale. In 1970, the U.S. Plant Variety Protection Act became law. The genetic tools for producing hybrid wheat allow for natural proprietary protection (i.e., seed from hybrid wheat cannot be economically replanted, due to the loss of hybrid vigor beyond the F_1 generation). The Plant Variety Protection Act provided propriety rights to the originator of a new cultivar. These two events were followed by greater activity on the part of the private wheat breeding industry (Briggle et al., 1982), which intensified in the mid-1970s because of development of specific chemicals that act as gametocides (now generally referred to as chemical hybridizing agents).

Even though considerable research has been directed toward developing hybrid wheat since the early 1960s, particularly by private industry, the 1974 and 1979 Wheat Cultivar Surveys showed that only a minor area had been devoted to hybrids (Reitz and Hamlin, 1978; Briggle et al., 1982). The hybrid wheat hectarage recorded in the 1979 survey amounted to $< 0.1\%$ of the total (Briggle et al., 1982). By 1984, hybrid wheat still made up $< 0.1\%$ of the U.S. wheat acreage (Siegenthaler et al., 1986). Kansas reported the seeding of about 0.3% of its wheat land to hybrids in 1985 (Johnson, 1985).

1-2.1.2 Canada

Wheat is the principal crop grown in Canada. In most years, about 95% of all Canadian wheat is grown in the Prairie provinces of Manitoba, Saskatchewan, and Alberta, primarily in their southern reaches (Peterson, 1965). Winters are long and cold; summers are short and hot. Rainfall is limiting, and droughts are common. The relatively low precipitation limits yield, but is an important factor in producing grain that is high in protein and of high baking quality. In Ontario, which produces 4% of Canada's wheat, and in other eastern provinces the climate is different. Rainfall is considerably higher, and more moderate temperatures and higher humidity prevail.

Most wheat grown in the Prairie provinces is HRS wheat. Winters are too severe for winter wheat production, except in southern Alberta and along the foothills of the Rocky Mountains (Peterson, 1965). Some HRW wheat, about 1% of Canada's production, is grown there, as is a small amount of soft white spring wheat (under irrigation). Soft white winter wheat is produced in Ontario, with minor amounts scattered across other eastern provinces. A very small amount of SRW wheat is also grown in the eastern provinces. Durum wheat makes up only about 5% of all wheat grown in the prairie provinces, but is an important export com-

modity. A minor amount of lower quality HRS wheat, known as *utility wheat*, is still marketed overseas, but is of declining importance.

Canada exported about 75% of the wheat it produced from 1979 to 1982, most of it HRS wheat. In 1984 the Canadian Wheat Board and Canadian Wheat Commission produced and test marketed a new type of high-yielding wheat, semihard in kernel texture. In the future, Canada may have a wider range of quality types available for export.

1-2.1.3 Mexico and Central America

Mexico and Guatemala are the only countries in this region that produce significant amounts of wheat. These countries currently harvest about 803 000 and 44 000 ha, respectively. Wheat yields in Mexico averaged 4.0 Mg ha^{-1} during the period from 1978–1982 (Table 1–1). A few Mexican farmers harvested as much as 8 Mg ha^{-1} (A. Valencia 1983, personal communication). Despite these high yields, Mexico, with rising incomes of the general population and heavily subsidized production, must still import about 15 kg of wheat per person to meet the needs of its rapidly growing population (CIMMYT, 1983).

Practically all wheat in Mexico is grown under irrigation, with the majority produced in the coastal valleys of the northwestern states of Sonora and Sinaloa. About 100 000 ha of wheat are grown in the central plateau, called the Bajío region, and some is grown in the rainfed highlands. Mexican farmers are highly sophisticated producers, using high-yielding, semidwarf cultivars and employing timely and up-to-date cultural techniques. Leaf rust (*Puccinia recondita* f. sp. *tritici*) and stem rust (*P. graminis* f. sp. *tritici*) are endemic in Mexico and can cause yield losses of 80 to 100% when young plants of a susceptible cultivar are attacked. Both leaf and stem rust are kept in check by frequent changes of cultivars and timely use of fungicides. Stripe rust (*P. striiformis*), Septoria nodorum and tritici blotches (*Leptosphaeria nodorum* and *Mycosphaerella graminicola*), barley yellow dwarf virus (BYDV), and head scab (*Fusarium* spp.) are sometimes a problem in the highlands.

In Guatemala, wheat is produced in the highland valleys under rainfed conditions. Yields average about 1.2 Mg ha^{-1} (Table 1–1). Because production conditions are usually wet, a number of diseases adversely affect the wheat crop, such as Septoria nodorum and tritici blotches, head scab, stripe rust, BYDV, and tan spot [*Pyrenophora tritici-repentis* (Died.) Shoem.]. Weeds are also a major production constraint.

1–2.2 South America

1-2.2.1 Andean Region

Wheat is a popular food source in the Andean region, but yields and production are low because of a number of interrelated factors. Roughly 250 000 ha of wheat are currently planted in the countries of Peru, Bolivia, Colombia, and Ecuador, primarily in the highlands, and yields average

about 1 Mg ha $^{-1}$ (Table 1–1). Consumption far exceeds domestic production, thus requiring the importation of some 2 Tg annually. At 40 kg per capita, this constitutes a high level of imports. Most governments in the area are contemplating changes in their agricultural policies that will provide greater incentives for farmers to grow wheat. The question remains, however, whether locally produced wheats will be able to meet the quality standards of the region's milling and baking industries.

The major constraints on production are moisture availability, diseases, and poor cultural practices such as improper seedbed preparation, insufficient fertilization, and a lack of weed control. Most of the wheat is produced under rainfed conditions, and rainfall is highly variable from year to year, in both amount and distribution (P. C. Wall, CIMMYT, 1983, personal communication). The major wheat disease problems in the Andean highlands are stripe rust and BYDV. High-yielding spring wheats with good resistance to stripe rust are currently available (H. J. Dubin, CIMMYT, 1983, personal communication), and efforts are underway to offer improved agronomic practices to farmers.

1–2.2.2 Southern Cone Region

Almost 10 million ha of wheat currently are grown in the vast Southern Cone region, primarily in Argentina and Brazil. Yields vary from about 2 Mg ha^{-1} in Argentina to about 600 kg ha^{-1} in Brazil (Hanson et al., 1982). The countries of the Southern Cone all import wheat, except for Agentina, which is the largest wheat exporter in the developing world. Wheat is consumed in the region primarily in the form of bread and pastry products.

Wheat is grown in the Southern Cone in a variety of environments, ranging from the highly favorable *pampa húmeda* ("humid plains") of Argentina to the acid soil conditions of Brazil. Wheat is grown in the tropical Cerrado area, close to Brasilia, Brazil (15°S Lat) and as far south in Chile as 41°S Lat, near Puerto Montt (M. A. McMahon, CIMMYT, 1984, personal communication).

Production constraints vary greatly across locations. In Brazil, low and unstable yields are due to: (i) acid soils with high levels of soluble Al and strong P fixation; (ii) heavy disease pressure from the rusts and *Septoria* and *Helminthosporium* diseases such as *Cochliobolus sativus* (Ito et Kurib.) Drechs. ex Dastur, head scab, and powdery mildew (*Erisyphe graminis* DC.); (iii) variable rainfall, often too much, particularly at harvest; and (iv) unseasonable frosts. An ongoing, aggressive research program is helping to mitigate some of these problems. High-yielding, Al-tolerant, disease-resistant, and lodging-resistant cultivars have been recently released, and are expected to have a major impact on Brazilian wheat production in the not too distant future (Hanson et al., 1982).

Argentina's greatest production constraints are variable rainfall (both amount and distribution) and lack of a stable supply of fertilizer. Steps are now underway to increase greatly Argentina's capacity for manufac-

turing fertilizer. The most immediate need is increased production capacity for N and P.[1] Argentina grows primarily high-yielding, semidwarf wheats of true spring or facultative growth habit. (Facultative growth habit, also known as semi-winter or semi-spring, is intermediate to spring and winter habit; facultative genotypes require some low-temperature vernalization, but less than true winter types.) These cultivars are generally classed as long cycle (May–June planting), intermediate cycle (July planting) and short cycle (August or later planting). Diseases can limit production, but most commercial cultivars are resistant to stem, leaf, and stripe rusts. Better resistance is needed against Septoria tritici blotch, head scab, and bacterial blight or streak (*Xanthomonas campestris* pv. *translucens*) (H. J. Dubin, CIMMYT, 1984, personal communication).

Chile's wheat area is now increasing, due to enlightened agricultural policies that are providing farmers with incentives to grow more wheat and an aggressive research program that is supplying new, more productive cultivars and improved production practices (M. M. Kohli, CIMMYT, 1984, personal communication). Uruguay and Paraquay are minor producers in the Southern Cone region (360 000 and 58 000 Mg, respectively, in the period from 1979 to 1982) (Table 1–1).

1–2.3 Western Europe

Wheat is a major crop in the Western European countries of France, Spain, Portugal, Italy, Switzerland, the Federal Republic of Germany (West Germany), Belgium, Netherlands, Denmark, and the United Kingdom. The majority is grown in France, West Germany, Italy, and the United Kingdom. The season for growing wheat is long, generally 10 to 11 months, beginning in October or November and ending in August or early September. Winters are generally long, cloudy, cold, and wet; summers are cool. The grain can be classed as SRW wheat of generally low quality, due to low protein content and poor gluten strength. Spring wheat is grown on $< 10\%$ of the area. Lodging is a persistent problem, but in recent years cultivars with much shorter and stiffer straw have begun to appear in commercial fields. With taller cultivars, it is common for farmers to spray the crop with chemicals to inhibit plant growth and thus reduce the adverse affects of lodging. The use of NPK fertilizer in Western Europe is heavy.

About 15 million ha of wheat are grown in Western Europe, including Spain and the United Kingdom. Yields are quite variable, from 1.7 Mg ha^{-1} in Spain to 6.5 Mg ha^{-1} in the Netherlands (Table 1–1). France averaged 5.0 Mg ha^{-1} on 4.5 million ha for the 3-yr period 1979 to 1982. During that same period, France, West Germany, and Spain together averaged exports of about 12.5 Tg. (Of this, France accounted for about

[1] Borlaug, N.E. 1984. The role of the agricultural sector in the economic recovery of Argentina. Consulting report to the Secretary of Agriculture of Argentina in Buenos Aires. Unpublished.

11.3 Tg.) On a regional basis, Western Europe exported about 22% of its total production.

Such diseases as head scab, stripe rust, leaf rust, Septoria tritici and nodorum blotches, and various root rots cause some losses each year, particularly on the Continent. Spraying with fungicides is commonly practiced to control these diseases.

1–2.4 Eastern Europe

The seven Eastern European countries of Bulgaria, Czechoslovakia, the German Democratic Republic, Hungary, Poland, Romania, and Yugoslavia grow about 10 million ha of wheat. Yields are generally high, ranging from 2.7 Mg ha $^{-1}$ in Romania to 4.1 Mg ha $^{-1}$ in Czechoslovakia. Production currently exceeds 31 Tg and, except for Hungary and Bulgaria, the countries of this region are net importers of wheat (Table 1–1).

The climate of Eastern Europe varies from oceanic to continental, with very cold and usually wet winters. The wheats grown are mostly winter habit types and are sown in the fall. Planting occurs during the months of September and October, and harvest occurs in July and August. In general, heavy use of NPK fertilizers is practiced; in some areas Ca and Mg fertilizers also are required. Pesticides are used heavily (CIMMYT, 1978).

Major constraints to production include diseases, lodging, and winterkill of plants. Droughts also occur in some years and can result in serious crop losses. The diseases reported most often are powdery mildew, *Fusarium* seedling blight and head scab, the three rusts, Septoria nodorum blotch, and foot rot or eyespot [*Pseudocercosporella herpotrichoides* (Fron) Deighton). Lodging often causes heavy crop losses and is now being combatted by shorter- and stiffer-strawed commercial cultivars and by the use of the plant growth regulator CCC [(2-chloroethyl) trimethylammonium chloride]. Most Eastern European countries have good wheat breeding programs, and rapid progress is being made toward the release of superior short-strawed, lodging-resistant cultivars. Higher yield per hectare is the most viable way to increase production in these countries.

In contrast with most of the wheat-producing regions of the world, in Eastern Europe wheat is used heavily as a feedgrain. The German Democratic Republic uses more than 50% of its production for feed purposes; the remainder is used for bread.

1–2.5 Union of Soviet Socialist Republics

Wheat is the number one crop in the USSR. Wheat constitutes nearly 90% of the USSR's food grain production and half the total grain production for food and feed combined (U.S. Central Intelligence Agency, 1974).

Most of the agricultural land of the USSR is similar in climate to

that cultivated in Canada and the North Central states of the USA. The growing season in most of the USSR is short. Late frosts and early snows are common in the major wheat growing areas, which lie at the same latitudes as the Prairie provinces of Canada. Areas warm enough for better plant growth lack sufficient rainfall. Semidesert and desert areas dominate the southern USSR, which is at the same latitude as Tennessee (U.S. Central Intelligence Agency, 1974).

Variability of weather from year to year has a deleterious effect on agricultural production in the USSR. Even though the USSR has the most extensive agricultural land resources of any country in the world, yields are frequently diminished and sometimes crops are lost entirely because of drought, desiccating winds, or violent storms. A significant increase in production could be achieved through more irrigation, but water supplies are limited where needed, and considerable capital input would be required. A major agricultural asset is the broad belt of fertile Chernozem soil (Mollisols) that extends from the country's western border far beyond the Ural Mountains and into the New Lands area of Kazakhstan and western Siberia, which was brought into production in the 1950s (U.S. Central Intelligence Agency, 1974).

Both winter and spring wheat are grown in the USSR. The area planted to spring wheat is about 2.5 times that planted to winter wheat, which is concentrated in the western USSR, particularly in the Ukraine Republic (Fig. 1–6). Winter wheat is always vulnerable to some winterkill, but still is higher yielding than spring wheat grown in the same environment. The principal spring wheat area is east of the Volga region and extends into the New Lands area, where temperatures are severe during the winter.

Average yields have fluctuated considerably, but the general trend is upward. The USSR significantly increased support for agricultural re-

Fig. 1–6. Wheat-growing regions of the USSR.

search in the 1970s, particularly for wheat improvement. Because wheat production has been extended to the limits of the available suitable land, further production increases must come from improvements in the genetic yield potential of the cultivars grown, better pest control, and more effective management systems. For the period from 1979 to 1982, the USSR produced an average of 88.9 Tg on 58.9 Mha, with yields averaging 1.5 Mg ha^{-1}. An additional 14.3 Tg was imported during the same period to satisfy domestic needs (Table 1–1).

Most Soviet wheat is used for bread products. About 12% of the spring wheat area is planted to durum (U.S. Central Intelligence Agency, 1974). In addition to macaroni and spaghetti, a minor amount of durum is used for bread and cookie flour. An unknown amount of wheat, probably the lowest in quality, is fed to livestock. Most USSR wheat, particularly the spring wheat, is high in protein and has very good baking quality.

1–2.6 East Asia

The 29 million ha of wheat grown in China in 1983 constitutes the largest wheat area among the countries of the developing world. From 1979 to 1982, yields in China averaged 2.3 Mg ha^{-1} (Table 1–1), and in 1983, new records were set both for total production (84 Tg) and average yield (2.8 Mg ha^{-1}) (Lu, Liangshu, President, Chinese Agricultural Academy of Sciences (CAAS), Beijing, PRC, personal communication, 1984). Imports by China averaged some 12.3 Tg during the same period.

Wheat is grown throughout China, with most east of the 100th meridian. The three main wheat-growing regions, designated according to growth habits, are the northern winter wheat region, the southern winter wheat region (where spring and facultative types are sown in the fall), and the spring wheat region. These are further subdivided into 10 subregions (Fig. 1–7). Sixty percent of the total area is in the winter wheat region, and 40% is in the spring wheat area; the latter includes both true spring and facultative types (Zhuang, Qiaosheng, Institute of Crop Breeding and Cultivation, CAAS, Beijing, PRC, 1984, personal communication). Only 17% of the wheat (the northeastern spring region) is sown in the spring, the remainder being sown in the fall. White grain is preferred, but large quantities of red grain are produced. Wheats with semidwarf stature now predominate in China.

Environmental stresses vary across subregions. Spring drought and hot dry winds during the grain-filling stage of the crop are common in the northern and western wheat areas. In the central and southern wheat-growing areas, double- or triple-cropping in rice-wheat rotations are common. Wet soils and sprouting in the head are frequent production problems (Zhuang, Qiaosheng, 1984, personal communication).

One or more of the three rusts (leaf, stem, stripe) remain a constant source of concern throughout most of the 10 wheat regions of China, but no epiphytotics have been reported in recent years. Cultivars are frequently changed to guard against rust epiphytotics. Head scab is a dam-

Fig. 1–7. Wheat-growing regions of China.

aging disease in areas from the Yangtze River valley south. Measurable losses from head scab occur every year; severe infection and losses of 20 to 40% occur every 4 to 5 yr. New cultivars with improved resistance to head scab developed by breeding programs along the Yangtze River are nearly ready for release. Other serious diseases in China are powdery mildew, BYD, leaf blights and root rots, common bunt, loose smut, and snow mold. Aphids, armyworms, and various underground insects also cause losses in China's wheat crop (Liu, Zongzhen, Crop Protection Institute, Shanghai Academy of Agricultural Sciences, Shanghai, PRC, 1982, personal communication).

Wheat research, including breeding and agronomy, is receiving much attention at the various agricultural institutes across China. New cultivars are rapidly emerging and the practice of double- and triple-cropping is highly sophisticated. China, long a heavy user of organic fertilizers, is shifting rapidly toward high-analysis fertilizers, such as urea. In recent years, 13 large factories have been built, each with a production capacity of more than 1000 Mg of NH_3 per day. The increased emphasis on research and development, combined with current favorable governmental policy, is likely to push China's average wheat yield to more than 3 Mg ha^{-1} by the end of the 20th century.

In South Korea, wheat is produced primarily in a double-cropping sequence (with rice in the south and soybean in the northern upland

areas). Production is about 3.2% of consumption (Table 1–1). Major production problems are the wet acidic soils, diseases (*Helminthosporium* and *Fusarium* leaf blights, head scab, the rusts, certain viruses, and powdery mildew), and the late maturity of commercial cultivars currently in use, which makes it more difficult to double-crop and leads to heavy lodging (CIMMYT, 1977; CIMMYT, 1978). New early maturing, high-yielding, semidwarf wheats entering production in recent years have increased the area that can be sown to wheat. Researchers at three research stations, at Suweon, Honan, and Youngnam, work on wheat and barley breeding.

North Korea grows about 159 000 ha of wheat per year and, in recent years, has been importing slightly more than 0.5 Tg annually. Mongolia grows about 400 000 ha of wheat, but with a very low average yield of 0.7 Mg ha^{-1}.

1–2.7 South Asia

In South Asia, a vast wheat area of more than 30 Mha, wheat production continues to increase dramatically. The greatest amount of wheat is produced in the Ganges and Nurmada basins of India, and the upper tributaries of the Indus River of Pakistan. In India and Pakistan, a large part of the wheat area is irrigated. In Nepal and Bangladesh, wheat is mainly rainfed. Most of the wheat grown is spring habit, but sown in the fall and harvested in April and May. White grain varieties are generally preferred and grown.

Semidwarf, high-yielding cultivars were introduced into India in 1962, when the country's average annual production was about 11 Tg. Production reached 16.5 Tg in 1968, after considerable research, extension, and demonstration work was done to promote the use of new semidwarf cultivars. At that point, it was clear that a revolution in wheat production was underway. By 1984, wheat production in India reached nearly 45 Tg. With the excellent research program now underway, India expects to produce 50 Tg of wheat by about 1988 (Curtis, 1982). In the early 1980s, India was a net importer of wheat to maintain stockage levels. Most wheat is used for direct human consumption, primarily in the form of chapatis (an unleavened, griddle-baked bread).

A similar success story can be told for Pakistan. Production was about 3.9 Tg in 1966; by the early 1980s it averaged over 12 Tg. Nepal also shared in this revolution, but on a much smaller scale; the country now produces nearly 0.5 Tg on $<$ 400 000 ha (CIMMYT, 1983).

The wheat production figures for Bangladesh are likewise dramatic. In 1971, Bangladesh was growing about 126 000 ha of wheat, yielding $<$ 1 Mg ha^{-1}. By 1984, the wheat area had increased to about 647 773 ha and yields averaged 2.16 Mg ha^{-1} (Fig. 1–8). However, much of the additional area is devoted to an early maturing, Mexican spring wheat cultivar ('Sonalika') that is now susceptible to leaf rust, and if the Bangladesh revolution in wheat production is to continue, replacement cul-

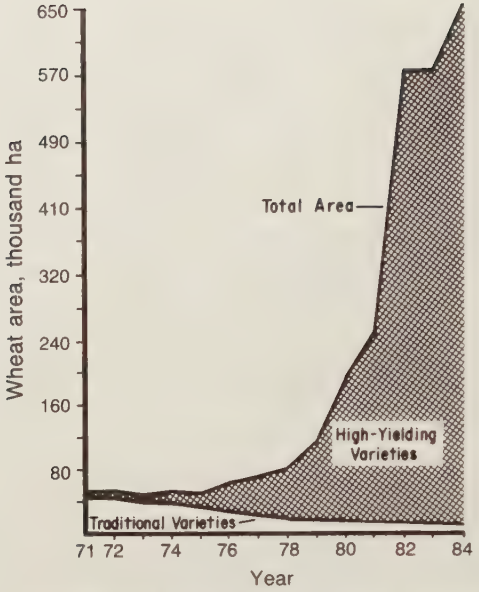

Fig. 1–8. Increase in total wheat area and use of high-yielding cultivars in Bangladesh, 1971 to 1984. Source: FAO Production Yearbooks.

tivars must soon be released (L. Butler, CIMMYT, 1983, personal communication).

The wheat revolution in these countries has a common thread, namely, the availability of well-adapted, high-yielding, disease-resistant, semidwarf cultivars; a coordinated training, research, and extension program; and a policy environment conducive to increased wheat production. These efforts continue unabated, and further increases in wheat production in South Asia are expected (Curtis, 1982).

The major threats to future wheat production in this region, assuming no drastic socioeconomic changes, are the ever-increasing salinity of irrigated areas and potential changes in disease virulence, particularly of leaf and stripe rust. The salinity problem is grave and overcoming it will require a huge engineering effort (drainage). With the continued release of resistant cultivars, which now appears to be happening, diseases can be controlled. The highly popular cultivar Sonalika, mentioned in reference to Bangladesh, is currently grown on more than 10 Mha throughout the region. Its susceptibility to leaf rust exposes not only Bangladesh but the entire South Asia region to potentially devasting crop losses. Similarly, stripe rust could cause grave losses in northern India and Pakistan. India, Pakistan, Nepal, and Bangladesh have aggressive breeding programs underway that should make possible the release of new cultivars intended to replace Sonalika and other old cultivars as they become susceptible.

1–2.8 Middle East

Wheat was grown extensively in Turkey, Iran, Afghanistan, Syria, Iraq, and Eastern Mediterranean countries on about 21 Mha in 1983. Although the Middle East is a large-producing area, every country (except Turkey) imports some wheat. Wheat consumption rates in several countries in this region are the highest in the world, averaging 225 kg per capita in 1981 (CIMMYT, 1981). Consumption is in many forms, such as leavened and unleavened breads and bulgar.

Diverse and variable climatic conditions characterize the region. There are two major agroclimatic zones where cereals are grown, Mediterranean and highland. The Mediterranean zone is characterized by hot, dry summers and cool, moist winters. Most crops are grown during the winter because of the season's relatively high rainfall. In the highland zone, much of which exceeds 1000 m in elevation, winters are cold and summers hot (ICARDA, 1983). With the notable exception of Turkey, the soils in this zone are generally shallow and cereal yields average about 650 kg ha^{-1}. Crops are generally planted in the fall, although spring plantings are important in parts of Turkey and Afghanistan.

The major constraints affecting wheat production are drought, diseases, insects, and weeds. Most of the arable land receives variable amounts of rainfall, ranging from only 200 to 600 mm yr^{-1}; distribution is highly variable as well. Only a small portion of the wheat area is irrigated.

Major diseases are the three rusts (leaf, stripe, and stem), Septoria tritici blotch, powdery mildew, common and dwarf bunts, loose smut, tan spot, and BYDV. Hessian fly and wheat stem sawfly cause significant losses in some years. Sunn pest and aphids are other insects of importance (J. M. Prescott, 1982, personal communication).

Common wheat is the major crop. However, durum wheat occupies a large area, particularly where rainfall is limited to 300 to 500 mm. It is primarily spring-habit wheats that are grown in the Mediterranean zone, although they are generally planted in the fall. High-yielding semidwarf cultivars predominate. Improved (moisture-conserving) cultural practices have been generally adopted in this zone, but further improvements are needed to realize more fully the genetic potential of the high-yielding cultivars. In the highland zone, there is still a great need for improved cultivars of the facultative and winter types. For the most part (excluding Turkey), cultural practices remain primitive, resulting in low yields.

1–2.9 North and West Africa

About 21 Mha of wheat are grown in Algeria, Egypt, Libya, Morocco, Tunisia, Angola, and Nigeria. Except in Egypt, the crop is rainfed and yields average about 850 kg ha^{-1}. Because most of the wheat produced

in Egypt is grown under irrigation, yields there average more than 3.0 Mg ha^{-1}. None of the countries in this region are self-sufficient in wheat. Net imports average about 11 Tg for the region (some 119 kg per capita) (Table 1–1).

In North Africa, the total cereal-growing area is about 50% durum wheat and 20% common wheat, with barley occupying most of the remaining area. Wheat is grown as a winter crop, which coincides with the rainy season. It is planted in the fall and harvested in May or June.

Major hazards to the North Africa crop include the amount and distribution of rainfall, diseases and insects, and lack of adoption of improved cultural practices. During the wetter years, Septoria tritici blotch and stripe rust diseases can cause severe damage. Other prevalent diseases include stem rust, powdery mildew, tan spot, and root rots. Hessian fly can cause significant losses, particularly in Morocco, as can wheat stem sawfly in several countries. Aphids and nematodes also are periodic problems.

Wheat is a relatively new crop in West Africa. Nigeria, Angola, Mali, and Senegal could grow fairly significant amounts of wheat if heat-tolerant cultivars were available. Moreover, policy makers would have to decide to favor wheat over other crops. Heat tolerance is the overriding cultivaral requirement for these areas, and frequent irrigation is necessary due to high evapotranspiration rates. The season is short, mid-November to early March.

1–2.10 East and East Central Africa

Most of the wheat in East and East Central Africa is grown at high elevations (above 1500 m); near the equator it is grown at elevations of 3000 m or more. Wheat is generally produced under rainfed conditions, except in the lowlands of Somalia, Zambia, Botswana, and Zimbabwe, where irrigation is practiced. Rainfall in the highlands varies considerably from season to season and distribution within seasons is often unfavorable for wheat. The average annual rainfall is between 600 and 700 mm and generally falls from June to September. Less than 500 mm of moisture per cycle is considered marginal for wheat production. Soils are generally low in N and P and in some minor elements.

Wheat is usually planted in May to July and harvested in September or October. In Kenya, a second wheat crop is sometimes grown. Common wheat is grown in most of the region, except in Ethiopia, where durum wheat is grown on 60 to 70% of the area.

Production constraints in Ethiopia, especially for the small farmer, are the lack of improved farm implements and the short supply of fertilizers and high-yielding, disease-resistant cultivars. Weeds cause measurable yield reductions every year. Yields in Ethiopia average about 800 kg ha^{-1} (Table 1–1).

The main diseases in the highlands are stripe rust and Septoria blotches, particularly Septoria tritici blotch. Stem rust can devastate com-

mon wheat in Kenya and durum wheat in Ethiopia. Tan spot appears to be increasing in importance. Other diseases important in some years are common bunt, loose smut, BYDV, and bacterial leaf blight. In Tanzania, Zimbabwe, and Zambia, foliar and head diseases are of prime importance, though stem rust and leaf rust also are important. Diseases are negligible in Sudan but water availability for irrigation is an increasing problem (E. Torres, CIMMYT, 1984, personal communication). In Ethiopia, Kenya, Tanzania, and Zambia, there exists enough land with environments suited to wheat production for these countries, in theory, to become self-sufficient in wheat. It appears that this could be achieved, should these countries adopt agricultural policies favorable to the domestic production of wheat and decide to control population.

1–2.11 South Africa

Wheat area in South Africa has increased from an average of 1 197 000 ha for the 1961 to 1965 period to about 1 800 000 ha during the early 1980s. Slightly more than 2 Tg yr^{-1} was the average production in 1982 and 1984 (CIMMYT, 1983; 1985). Yield per hectare is low, averaging 0.7 Mg ha^{-1} in the 1961 to 1965 period and slightly above 1.0 Mg ha^{-1} in the 1980 to 1984 period. Low yields are a result of low rainfall in the Transvaal, the winter wheat area, and poor soils in areas of heavier rainfall.

Stem rust is the most important winter cereal disease (CIMMYT, 1978). Leaf rust and Septoria are common but generally have little effect on yield. Root diseases such as those caused by *Geaumannomyces*, *Fusarium*, *Rhizoctonia* and *Periconia* spp. occur. Under favorable conditions for the pathogens, stem rust and root diseases together can reduce yields by 50% or more. Aphids can cause severe damage in some years.

Planting times vary from April to August to September except in the northern Transvaal, where planting occurs during February to March and is harvested in July. The rest of the crop is harvested from November to January.

All the wheat produced is for human consumption, utilized as bread, cakes and pastries, cookies, and semolina products, the last from a small durum crop. South Africa is largely self-sufficient in wheat.

1–2.12 Oceania

The wheat-producing areas of Australia have gradually increased during the past 25 yr, from 3.6 million ha in 1958 to 12.7 million ha in 1983. Most wheat is grown in the arcuate belt of land curving across the eastern and southern regions where winter rainfall (some 250 to 650 mm in May through October) is sufficient to produce a crop. Spring habit wheat is grown, but is sown in late fall (May–June) and harvested in early summer (November–December).

Wheat yields are low and year-to-year variability is high in the Aus-

tralian wheat belt, compared to other major wheat-producing countries. At 1.7 Mg ha^{-1}, the 1983 average yield was higher than usual. Yields typically range from 1.2 to 1.4 Mg ha^{-1}. Although production has increased rapidly in the 1970s, this has been primarily due to an expansion of area, especially in New South Wales and Western Australia. Average yields increased by only 0.3% in the period from 1965 to 1983.

Constraints to production include low soil fertility, diseases (stem rust, stripe rust, Septoria blotches, take-all, and nematodes), and limited adoption of improved cultural practices. Application of N (through pasture farming methods) and P give good crop responses. Improved disease resistance in the semidwarf cultivars, which now cover over 50% of the total wheat area in Australia, is helping to overcome disease constraints. Considerable research in the areas of genetics, cultural practices, and chemical treatments is being directed at the Australian production constraints and should result in continuing increases in the country's wheat production.

Approximately 80% of the wheat produced in Australia is exported. The remainder is used both for direct human consumption (15%) and for feeding livestock (5%).

In New Zealand, wheat is a major crop but is grown on only 80 000 to 100 000 ha annually, most of which is found on the eastern side of the South Island. Stripe rust and Septoria tritici blotch are important diseases. Yields are high, with a national average of more than 3.9 Mg ha^{-1} in recent years. Both winter and spring habit wheats are grown.

1–3 WHEAT PRODUCTION IN THE FUTURE

Global population is predicted to reach between 8 and 10 billion people early in the 21st century. The implications of this eventuality are numerous and complex, not the least of which will be the need to double the supply of food during the next 30 to 40 yr, just to keep pace with population growth. Wheat, rice, and maize together provide about three-fourths of the calories and half of the protein requirements of humankind (Johnson, 1982). As a leading global food source, wheat will no doubt become even more important, which underscores the need to rapidly and continuously increase production. Greater wheat production can be achieved in two ways only: (i) by expanding the area sown, and (ii) by improving the yield per unit of area sown. Significantly more wheat could be made available for consumption by reducing the tremendous pre- and post-harvest losses that occur worldwide.

1–3.1 Expansion of Area

The world's wheat area is likely to expand somewhat during the next 20 to 30 yr, primarily by moving wheat into marginal production environments where it has not been a traditional crop. Significantly in-

creased use of productive agricultural lands for growing wheat is not likely, however, due to ever greater competition from other agricultural and nonagricultural uses.

The extent to which wheat can be grown in the more marginal (nontraditional) areas depends on several factors. Breeders and agronomists are now seeking to develop suitable cultivars and production technologies that would allow wheat to be grown successfully under adverse conditions, such as in acid soils and in more tropical environments. A limited number of improved cultivars already have been developed (through a cooperative program between Brazil and CIMMYT) that yield twice as much as traditional cultivars under Brazil's acid soil conditions. The success of this ongoing joint breeding effort results from crossing Brazilian wheats, which have genetic tolerance to high levels of free aluminum (a common characteristic of acid soils), with Mexican semidwarf spring wheats, which have high genetic yield potential and good disease resistance.

Current evidence also suggests that it is possible to breed wheats with greater heat tolerance and shorter growth cycles, which would enable their cultivation in more tropical areas (during the coolest season of the year). As these wheats are developed, appropriate production technologies must evolve simultaneously that are relatively site-specific, addressing such agronomic problems as too little or too much water, the control of pests (diseases, weeds, insects, vermin), and how best to apply fertilizer.

Social and economic incentives that encourage farmers to adopt new agricultural technologies also are necessary. New agricultural technologies must be profitable before they will be adopted and since most potential wheat farmers in the nontraditional areas operate at a subsistence level, profitability under their circumstances must be demonstrated clearly. In addition, governments must develop the infrastructure needed to facilitate both the distribution of inputs to farmers and the delivery of their increased production to market.

1–3.2 Improving Yields

For the foreseeable future, increased wheat production must come from higher yields (Johnson, 1982). Greater yield per unit of area sown can be achieved in two ways: (i) by using improved agronomic practices, and (ii) by developing better wheat plants (higher genetic yield potential, improved disease resistance, and greater tolerance to environmental stresses).

In many developing countries, on-farm research is showing that, in specific instances, wheat yields can be doubled or even tripled by controlling weeds more effectively and by applying fertilizer and/or other inputs (P. Wall and H. Hepworth, 1984, personal communication). As noted above, recommended agronomic practices must be appropriate for the circumstances of the farmers who are to use them, and a considerable

amount of site-specific, on-farm research will be necessary to develop and demonstrate improved production technologies.

The second and longer term avenue for raising yields is through the improvement of the wheat plant itself. Some wheat scientists speculate that a yield plateau is being approached (a few believe it had already been reached as of 1985). A more realistic appraisal indicates that wheat breeders have yet to fully utilize the genetic variability within the *Triticum* spp. (Briggle, 1982; Curtis, 1982; Johnson, 1982).

There is now a greater awareness among wheat scientists of the value of mixing up the germplasm base. Breeders appear increasingly inclined to intercross the wheat germplasm pools, especially the winter and spring wheat pools. The crossing of germplasm obtained from numerous, and very different, locations around the world also is on the increase. This exchange of germplasm is likely to occur with greater frequency in the future, unless hampered by the adoption of more restrictive quarantine laws (which at this writing unfortunately seems on the increase).

Interspecific and intergeneric crosses are receiving greater research attention in an effort to broaden the genetic base. Recent advances in chromosome identification by the use of various banding techniques, gel electrophoresis, and the like along with the development of procedures that open up new possibilities for chromosomal exchanges between related species, hold considerable promise for contributing to conventional wheat breeding programs. The scientist's ability to introgress individual genes, as well as blocks of genes, from related genera is continually increasing. Broadening the genetic base of the *Triticum* spp. via intergeneric hybridization and other genetic engineering techniques should provide the variability needed to greatly boost the genetic yield potential of wheat. Genetic engineering techniques will complement but not replace conventional plant breeding and genetics (Curtis, 1982; Johnson, 1982).

Great strides have been made in raising wheat production from the 1960s through the 1980s and most of this success, both in developed and developing countries, is the direct result of investments in wheat research. It is also clear, however, that global wheat consumption has kept pace with our ability to produce, and that the consumption of wheat and wheat products in the Third World has risen at a startling rate. While the developed, wheat-exporting countries will continue to play a vital role in meeting this growing demand, wheat production in the Third World must increase as quickly as possible. The achievement of higher levels of production on a global basis will require significant investments in research with no guarantees of when or even whether payoffs will be forthcoming. But these investments must be made. Past successes give a clear indication of the potential contributions of agricultural scientific research. While the pace of progress is likely to be steady in the case of wheat, the rapid gains from the 1960s to the 1980s will probably give way to incremental advances. Even so, the needs of a burgeoning world population make *all* advances in food production imperative.

REFERENCES

Briggle, L.W. 1980. Origin and botany of wheat. p. 6–13. *In* E. Häfliger (ed.) Wheat. Documenta Ciba-Geigy, Basel, Switzerland.

----. 1982. Potential for use of related species of wheat. p. 85–91. *In* Proc. Natl. Wheat Research Conf., Beltsville, MD, 26–28 October. National Association of Wheat Growers Foundation, Washington, DC.

----, S.L. Strauss, D.E. Hamilton, and G.A. Howse. 1982. Distribution of the varieties and classes of wheat in the United States in 1979. USDA Statistical Bull. 676. U.S. Government Printing Office, Washington, DC.

Bushuk, W., and C.W. Wrigley. 1974. Proteins: Composition, structure and function. p. 119–145. *In* G. E. Inglett (ed.) Wheat: Production and utilization. AVI Publishing Co., Westport, CT.

CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo). 1977. CIMMYT Report on Wheat Improvement 1977. CIMMYT, Mexico, DF, Mexico.

----. 1978. CIMMYT Report on Wheat Improvement 1978. CIMMYT, Mexico, DF, Mexico.

----. 1981. World wheat facts and trends. Report one: An analysis of changes in production, consumption, trade and prices over the last two decades. August. CIMMYT, Mexico, DF, Mexico.

----. 1983. World wheat facts and trends. Report two: An analysis of rapidly rising third world consumption and imports of wheat. October. CIMMYT, Mexico, DF, Mexico.

----. 1985. World wheat facts and trends. Report three: A discussion of selected wheat marketing and pricing issues in developing countries. October. CIMMYT, Mexico, DF, Mexico.

Cotton, R.H., and J.G. Ponte, Jr. 1974. Baking industry. p. 199–332. *In* G. E. Inglett (ed.) Wheat: Production and utilization. AVI Publishing Co., Westport, CT.

Curtis, B.C. 1982. Potential for a yield increase in wheat. p. 5–19. *In* Proc. Natl. Wheat Research Conf., Beltsville, MD, 26–28 October. National Association of Wheat Growers Foundation, Washington, DC.

Dalrymple, D.G. 1986. Development and spread of high-yielding varieties of wheat in developing countries. Bureau for Science and Technology, Agency for International Development. U.S. Government Printing Office, Washington, DC.

Häfliger, Ernst. 1980. Editorial. p. 3. *In* E. Häfliger (ed.) Wheat. Documenta Ciba-Geigy, Basel, Switzerland.

Hanson, H., N.E. Borlaug, and R.G. Anderson. 1982. Wheat in the third world. Westview Press, Boulder, CO.

ICARDA (International Center for Agricultural Research in the Dry Areas). 1983. Better harvests in dry areas. ICARDA, Aleppo, Syria.

Inglett, G.E. 1974. Wheat in perspective. p. 1–7. *In* G. E. Inglett (ed.) Wheat: Production and utilization. AVI Publishing Co., Westport, CT.

Johnson, M.E. 1985. Distribution of Kansas winter wheat varieties, 1976–1985. Kansas Crop and Livestock Reporting Service, Topeka, KS.

Johnson, V.A. 1982. New horizons in cereal production. p. 1–11. *In* E. J. Gallagher (ed.) Cereal production. Butterworth, in association with the Royal Dublin Society, Dublin, Ireland.

----, L.W. Briggle, J.D. Axtell, L.F. Bouman, E.R. Leng, and T.H. Johnston. 1978. Grain Crops. p. 239–255. *In* M. Milner et al. (ed.) Protein resources and technology. AVI Publishing Co., Westport, CT.

Leonard, W.H., and J.H. Martín. 1963. Cereal crops. The Macmillan Co., New York.

Miller, D.L. 1974. Industrial uses of wheat and flour. p. 398–411. *In* G. E. Inglett (ed.) Wheat: Production and utilization. AVI Publishing Co., Westport, CT.

Nuttonson, M.Y. 1955. Wheat-climatic relationships and the use of phenology in ascertaining the thermal and photo-thermal requirements of wheat. American Institute of Crop Ecology, Washington, DC.

Percival, John. 1921. The wheat plant, a monograph. E.P. Dutton and Co., New York.

Peterson, R.F. 1965. Wheat botany, cultivation and utilization. Interscience Publishers, New York.

Pfeiffer, W.H. 1983. Yield performance, yield stability and adaptation of spring wheats on a regional and global level. Analysis of a series of international variety trials across 15 years and 973 environments. Ph.D. diss. University of Hohenheim, Stuttgart.

Reitz. L.P. 1967. World distribution and importance of wheat. *In* K. S. Quisenberry and L. P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:1–18. Madison, WI.

———. and W.G. Hamlin. 1978. Distribution of the varieties and classes of wheat in the United States in 1974. USDA Statistical Bull. 604. U.S. Government Printing Office, Washington, DC.

Saunders, R.M., H.G. Walker, Jr., and G.O. Kohler. 1974. Feed uses of wheat and its products. p. 384–397. *In* G. E. Inglett (ed.) Wheat: Production and utilization. AVI Publishing Co., Westport, CT.

Siegenthaler, V., J.E. Stepanich, and L.W. Briggle. 1986. Distribution of the varieties and classes of wheat in the United States in 1984. USDA Statistical Bull. 739. U.S. Government Printing Office, Washington, DC.

U.S. Central Intelligence Agency. 1974. USSR Agricultural Atlas. U.S. Government Printing Office, Washington, DC.

USDA. 1984. Foreign agriculture circular-grains. FG-6-84. U.S. Government Printing Office, Washington, DC.

———. 1985. Wheat outlook and situation report. Economic Research Service, WS-273, September. p. 27. U.S. Government Printing Office, Washington, DC.

U.S. Department of Commerce, 1978. Census of agriculture. Bureau of the Census. Vol. 4. U.S. Government Printing Office, Washington, DC.

Woodhams, A.R. 1980. The world wheat market and its problems. p. 85–90. *In* E. Häfliger (ed.) Wheat. Documenta Ciba-Geigy, Basel, Switzerland.

2 Morphology and Anatomy of the Wheat Plant

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Wheat (*Triticum aestivum* L. em. Thell.) has received considerable morphological and anatomical study because of its economic importance. The first summary of the accumulated knowledge of both vegetative and reproductive parts of wheat was by Percival (1921), who also included an impressive amount of careful original research. His monograph remains useful and a necessary starting point for investigators even today.

The morphology chapter in the first edition of this book (Briggle, 1967) included findings from many investigations since Percival but during the past 20 yr (1965–1985) studies have become steadily more detailed and sophisticated with the introduction of resin techniques for light microscopy and transmission- and scanning-electron microscopy.

All organs and structures of wheat for which morphological and anatomical information is available are covered in this chapter. More than 80% of the studies on which this chapter is based have been done since the first edition of this book was published. It will become evident that while there are still blanks on the anatomical map, intensive research in some areas has uncovered structural detail and complexity undreamed of at the time of Percival's monograph, and even long after.

2–1 MATURE VEGETATIVE STATE

2–1.1 General Morphology

The shoot is a short rhizome bearing several axillary leafy culms (tillers) that may each grow to about a meter in height (Fig. 2–1). The number of culms varies with cultivar, planting depth and density, and external conditions. Each culm has five to seven nodes. Only three or

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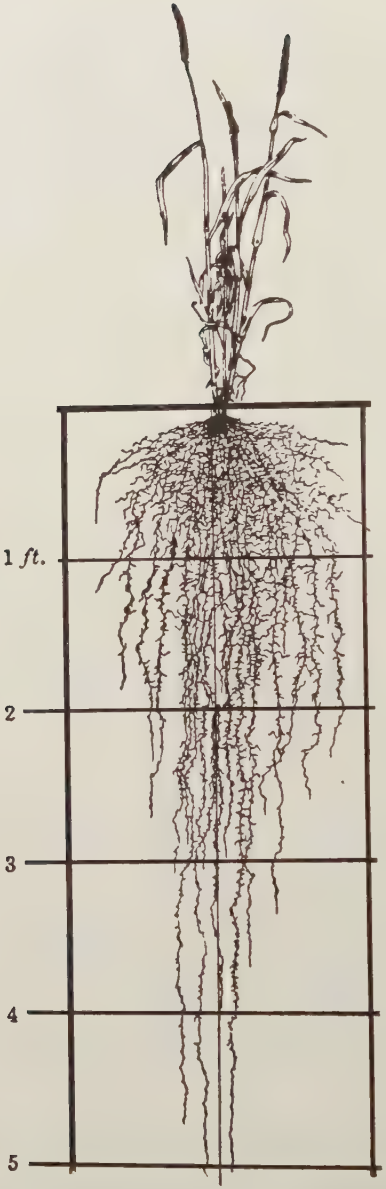

Fig. 2–1. A wheat plant at time of flowering. From Hayward (1938), with permission.

four foliage leaves develop, though, because the lower internodes are short and often at or below the soil surface. The uppermost, or flag leaf, subtends the inflorescence.

Each culm produces an inflorescence, which is a thick, condensed branch system. The basic unit of this *spike*, as it is called, is the *spikelet*,

within which are borne the specialized flowers (florets) typical of grasses. The inflorescence is described more fully in section 2–3.1.

The diffuse root system consists of adventitious roots (including the so-called *seminal* embryo roots) that branch and rebranch to form several orders of slender roots. Some roots extend horizontally for 30 to 35 cm just below the surface; others grow diagonally downward within the top 30 cm of soil. Below 30 cm, however, fewer and less branched roots extend vertically to 150 cm or deeper.

2–1.2 Mature Foliage Leaf

2–1.2.1 Gross Morphology

Each leaf of wheat, as in most other grasses, has a stem-ensheathing tubular base instead of a petiole. The conspicuous swordlike blade portion therefore juts out one node above the true node of leaf attachment. The leaf base encircles the node where it is attached for more than 360° and extends upward as a tubular sheath around the internode to the next node, where it turns abruptly outward in the form of a flattened blade (Fig. 2–2). A short, membranous, collarlike extension of the sheath where it turns outward is called the *ligule*. Two membranous, curved, clawlike projections at the base of the blade are called *auricles*. The base of the leaf sheath, just above the node of attachment, is a thickened, gravity-sensing pulvinus (Fig. 2–7).

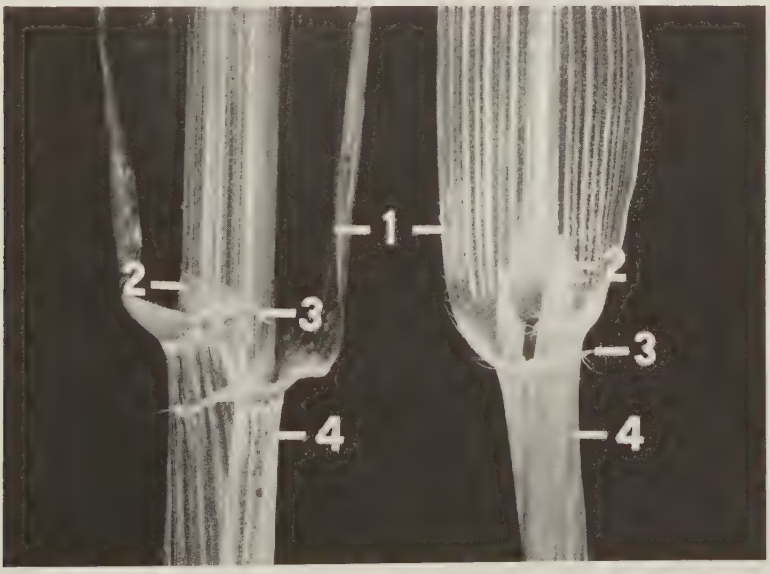

Fig. 2–2. Foliage leaf. *1*, Blade; *2*, Ligule; *3*, Auricle; *4*, Sheath. Culm has been removed in photo on the right. ca. × 2.

2-1.2.2 Leaf Epidermis

The upper (adaxial) blade epidermis forms ridges over the major longitudinal vascular bundles. An adaxial surface view (Fig. 2–3) shows rows of cells elongated parallel to the leaf axis. Long cells above and adjacent to these ridges are interspersed with short prickle hairs, which also occur on the margin. Some cultivars have more and/or longer hairs (Pal et al., 1952). Short cells containing silica bodies are interspersed among the long cells, either alone or paired with cork cells (Blackman, 1969).

Bands of large bulliform (i.e., "balloonlike") cells, three to seven cells wide, occur in the adaxial furrows. Such cells are common among grasses. They are often said to be able to lose water, thus reducing their volume, which supposedly causes a leaf to curl, thereby decreasing transpiring surface area, but evidence for this is unconvincing (Esau, 1965).

Stomata occur in rows on both surfaces. They are more common above than below, and are most frequent near the leaf base and sparsest near its tip (Teare et al., 1971). Stomata are most numerous per unit area on the first leaf, and are progressively fewer on successive leaves. Each stomatal apparatus consists of two bone-shaped guard cells, each flanked by a large subsidiary cell (Fig. 2–3, 2–4, 2–6). When open, the pore is an elongate slit; when closed it is merely a thin line, since the shanks of the guard cells touch (Fig. 2–4). This unusual stomatal organization is typical of grasses; it differs considerably from the familiar kidney bean stomatal shape of other groups of plants. A substomatal chamber underlies each stomatal apparatus (Fig. 2–6, 2–8). As in most plants, the epidermis lacks chloroplasts except in guard cells, where their presence is related to the mechanism for controlling pore opening and closing.

The leaf surface has a dense epicuticular wax coating (Fig. 2–4). At

Fig. 2–3. Adaxial (upper) surface of leaf blade. *a*, Prickle hair. *b,c*, Rows of stomata; *e*, Rows of bulliform cells; *n*, Optical section of underlying mesophyll cells. From Percival (1921). × 20.

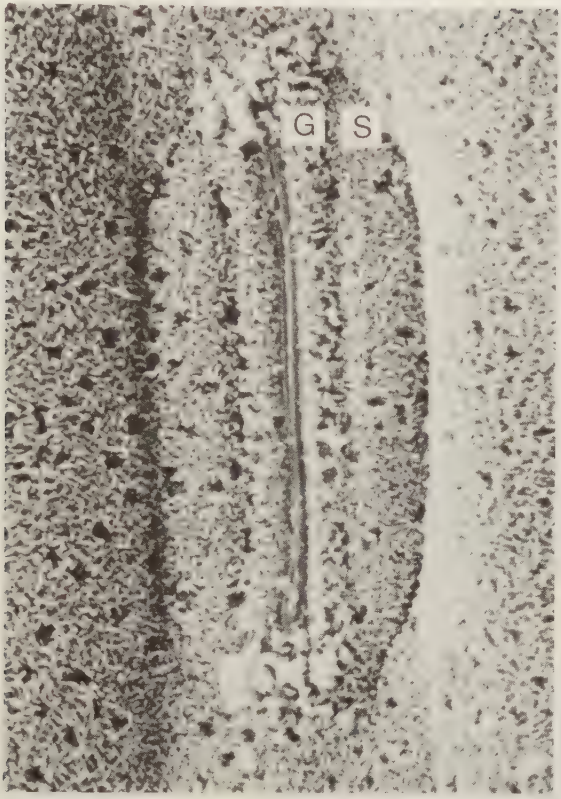

Fig. 2–4. Scanning electron micrograph of stomatal apparatus. *G*, Guard cell; *S*, Subsidiary cell. Stoma is closed. Epicuticular wax is evident as an outer coating of irregular rodlets. From Troughton and Donaldson (1972), with permission.

high magnification it is seen as randomly overlapping tubes (Fig. 2–5) averaging 0.1 μm in diameter and 5 μm in length (Wettstein-Knowles, 1974). Coiled wax ribbons also occur among the tubes. This is only one of many patterns of wax deposition on leaves, which in general has been linked to diffusion and reradiation of intense solar radiation.

2-1.2.3 Mesophyll

The leaf interior, excluding vascular bundles, is called the *mesophyll.* It consists of three to five layers of rather homogeneous parenchyma cells rich in chloroplasts (Fig. 2–6). Each mesophylll cell has from 1 to 10 lobes; the lobe pattern determines the ratio of internal mesophyll surface area per unit of leaf surface area. Some polyploid strains of wheat have less compact leaves than monogenomic strains, but they also have decreased internal mesophyll surface area. This may affect their physiological activity (Sasahara, 1982).

In the flag leaf, conspicuous oil globules (eleosomes), several per cell

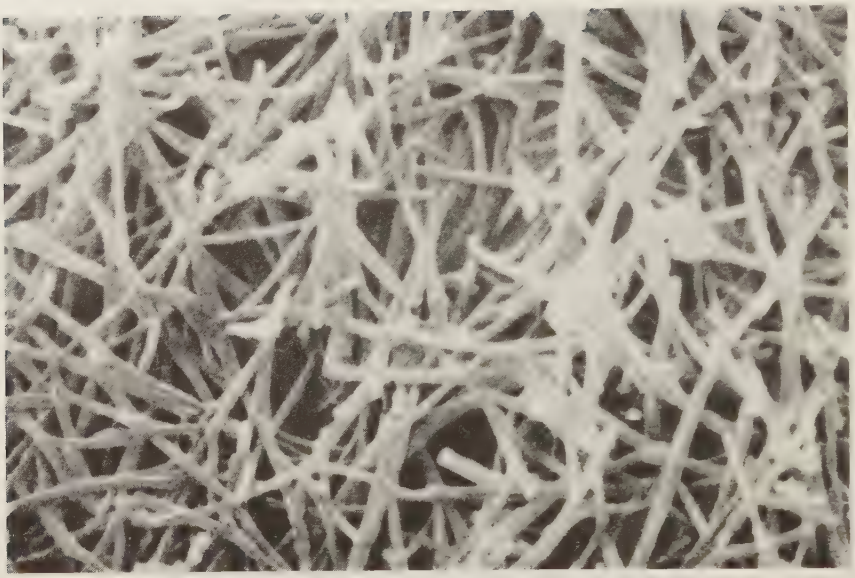

Fig. 2–5. Highly magnified view of epicuticular wax rodlets on leaf surface. From Troughton and Sampson (1973), with permission.

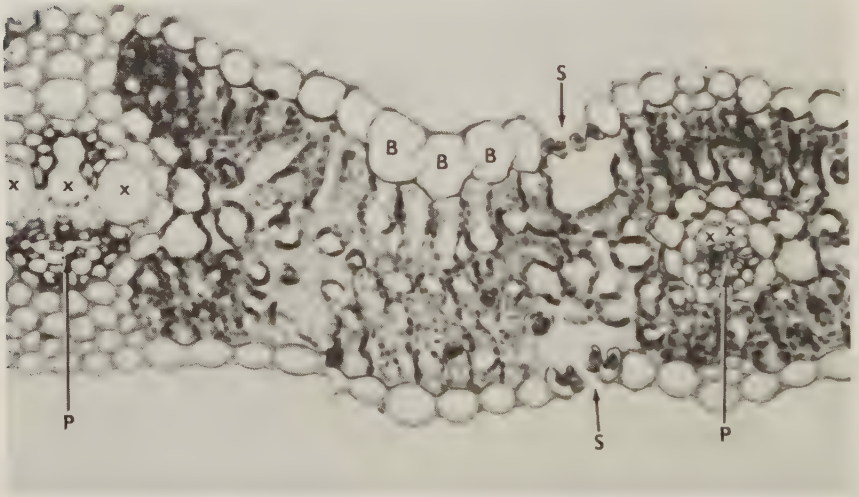

Fig. 2–6. Cross section of portion of a leaf blade. Stomata occur in both epidermises. Mesophyll is homogeneous. Large bundle (left) has bundle sheath extension to both epidermises, small bundle (*right*) lacks them. *X*, Xylem; *P*, Phloem; *B*, Bulliform cells; *S*, Stomata. × 120.

and up to 14 μm in diameter, form about 10 days after anthesis. They have been found to persist 40 days later (Parker and Murphy, 1981). They may provide temporary photosynthate storage, but a recent tracer study does not support this hypothesis (Murphy and Parker, 1984). Eleo-

somes have been verified in wheat and 20 other grasses with a double bundle sheath, but they have been reported absent in all but one of 21 grass species with a single bundle sheath (Chonan et al., 1984).

2-1.2.4 Pulvinus

The pulvinus is the modified base of the leaf sheath (Fig. 2–7). It retains the potential for cell enlargement after the rest of the leaf is mature. If a culm lodges, pulvinus cells on the lower side will elongate, but not divide (Bridges and Wilkins, 1973; Dayanandan et al., 1977), thus helping to right the culm. The pulvinus is thicker than the rest of the leaf sheath. Stomata, trichomes, and silica in the epidermis are absent in the pulvinus. Lignified cells are also absent, except for annular or helical xylem elements, and the bundle cap consists of collenchyma. Pulvinus parenchyma cells contain starch grains and/or calcium oxalate crystals thought to act as statoliths (i.e., balancing stones); thus, these cells may be gravity-sensing. Such cells are known as *statocytes* (Dayanandan et al., 1977; Prankerd, 1920).

2-1.2.5 Vascular Architecture

All vascular bundles occur more or less in the median plane of the leaf (Fig. 2–6, 2–8). The midvein is flanked in each blade half by equally large longitudinal bundles, usually five in number (Patrick, 1972a). All have fibrous bundle sheaths that extend as ridges to both surfaces (Fig. 2–6, *left bundle*). Between any two large bundles are one to three smaller longitudinal bundles lacking extensions (Fig. 2–6, *right bundle*) or with only a small adaxial extension. All longitudinal bundles are spaced about 150 μm apart (Blackman, 1971). Major bundles anastomose with each other toward the leaf tip, while the smaller ones merge more proximally

Fig. 2–7. 1, Intact node showing thickened leaf base. 2, Longisection through node; *a*, Thickened leaf sheath base (pulvinus); *b*, Solid nodal plate. Note hollow pith of internodes above and below node. From Percival (1921). × ½.

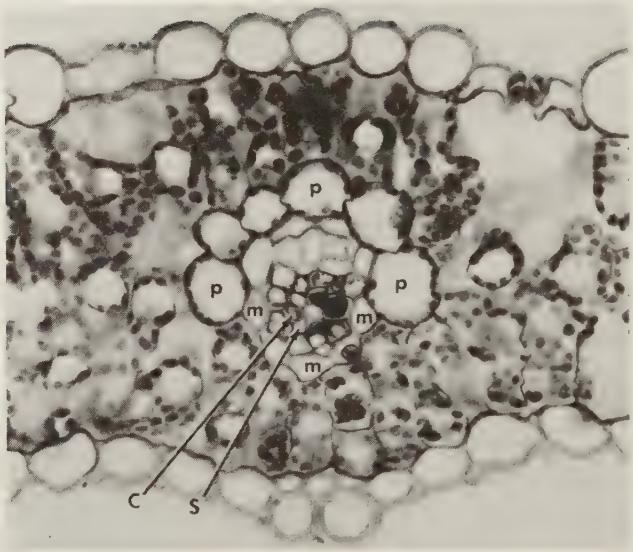

Fig. 2–8. Cross-section of leaf to show small longitudinal bundle. Sieve tube members (*s*) are smaller in diameter than companion cells (*c*). Mestome sheath cells (*m*) have walls thickened toward the vascular tissue. Outer parenchyma sheath (*p*) next to mestome is incomplete. × 180.

with each other or with major bundles. Most of the 27 to 31 large and small longitudinal bundles pass downward through the sheath and into the node (Patrick, 1972a). All major and minor longitudinal bundles are repeatedly cross-connected, except in the pulvinus, by many short cross veins (Blackman, 1971). Cross veins also are called *transverse veins* or *comissural veins.*

Longitudinal bundles are collateral, consisting of an adaxial strand of xylem and an abaxial strand of phloem (Fig. 2–6). Larger bundles have one or two annular or helical protoxylem elements, two large pitted metaxylem elements, and a few smaller vessels abutting the phloem (Kuo and O'Brien, 1974). Phloem consists of 7 to 10 wide sieve tubes sharply delimited from the adjacent slender companion cells. Small longitudinal bundles lack protoxylem and have only slender metaxylem elements. The sieve tubes are narrower in these bundles but their companion cells are wider (Fig. 2–8).

Phloem in large and small longitudinal bundles consists of typical thin-walled sieve tubes called *type 1*, and a different set of tubes called *type 2*, with lignified walls two to three times thicker than in type 1 (Kuo and O'Brien, 1974). Type 2 elements occur next to xylem vessels in all longitudinal bundles. It has been suggested that type 2 elements, and similar thick-walled cells found in the phloem of maize (*Zea mays* L.) and rice (*Oryza sativa* L.) leaves, may help to retrieve solutes from the xylem (Evert, 1980). Sieve tube members of wheat and other grasses lack

the typical P-protein of nongrasses but have instead plastids containing crystalloids (Eleftheriou, 1984). If a sieve tube cell is disturbed, these plastids rupture and the crystalloids plug the sieve plate pores, thus sealing them as P-protein does in dicots.

Longitudinal bundles have a double bundle sheath. The inner (mestome) sheath cells are lignified, with additional thickening on walls facing the vascular tissue (Fig. 2–8). They also have suberized lamellae embedded in their wall. Plasmodesmata are absent between mestome cells and xylem elements, but are abundant between mestome cells and metaphloem elements. Plasmodesmata connecting the mestome with phloem cells are far more abundant in small longitudinal bundles that differentiate after the leaf begins to export photosynthates, than in large bundles that differentiate during the earlier, energy-importing stage. O'Brien and Kuo (1975) calculated that 99% of the water flowing in leaf bundles diffuses into the mesophyll from only the seven largest bundles.

The mestome sheath contains only rudimentary chloroplasts, called *proplastids* (Bisalputra et al., 1969; Carolin et al., 1973). The adjacent outer parenchyma sheath has only small chloroplasts, and normal chloroplasts occur only in mesophyll cells. This is typical of C_3 grasses such as wheat (Waller and Lewis, 1979).

The wheat leaf reportedly transports water and photosynthates mostly in separate sets of longitudinal bundles. This seems to be controlled by mestome anatomy (Kuo and O'Brien, 1974; Kuo et al., 1974). The suberized lamellae in mestome cell walls may also prevent water and solute leakage, thereby forcing these substances to move through plasmodesmata (Kuo and O'Brien, 1974). The lamellae may therefore function as do transfer cell membranes in the minor veins of many plants. This could explain why transfer cells are unknown in grass leaves. Suberized lamellae form first in cells adjacent to protophloem and last in cells that abut on tracheary elements (O'Brien and Kuo, 1975).

The slender cross veins lack any sheath, and consist merely of one vessel with a single file of xylem parenchyma and one sieve tube with a single file of phloem parenchyma (Kuo et al., 1972). Companion cells are absent. The xylem vessel member wall is unusual in that it is uniformly thick and imperforate only where it contacts a sieve element or mesophyll cell, but it has a helical 2° thickening where it abuts a vascular parenchyma cell. It has been demonstrated, using ferric chloride solution ($FeCl_3$), that cross vein xylem transports water, but the water does not readily leak out (Kuo et al., 1972).

The entire vascular network of the wheat leaf, as in other grasses, is interconnected, without any of the free vein endings characteristic of dicots. The preceding description of the details of xylem and phloem structure indicates that movement of water and photosynthates, as well as the control of their direction of flow, differs from that in typical textbook discussions, which are usually based on work done with dicot leaves.

2–1.3 Mature Culm

The culm epidermis lacks bulliform cells but has all of the other cell types described earlier for the leaf epidermis. Stomata occur only in one or two rows just outside each of the several vertical strips of hypodermal chlorenchyma (Fig. 2–9). A conspicuous, separate lacuna (hollow pith) occurs in each internode, occupying 70 to 80% of culm volume.

The outermost 7 to 10 cortical cell layers form a continuous sheath of sclerenchyma fibers just below the epidermis. Embedded within this sheath are several vertical strips of chlorenchyma, each bisected by a small vascular bundle (Fig. 2–9). Each bundle in this peripheral vascular ring has an incomplete inner mestome and outer parenchyma sheath. This sheath forms only where the bundle is in contact with chlorenchyma. Between the sclerenchyma sheath and the large central lacuna (hollow pith) are several layers of sclerified parenchyma cells, among which there is an inner ring of large vascular bundles. The bundles in this ring lack an outer sheath (Fig. 2–9).

Parenchyma tissue laced with horizontal vascular bundles forms a solid disc at each node (Fig. 2–7). The culm is therefore light in weight, because of the lacuna, but strong because of the cortical fiber sheath and the nodal discs.

Vascular bundles in the culm are arranged predictably in each node and internode (Patrick, 1972a, 1972b). Each leaf contributes 27 to 31 longitudinal bundles to the node where it is attached, and another 34 to 48 culm bundles enter the node from the internode above. All leaf-derived

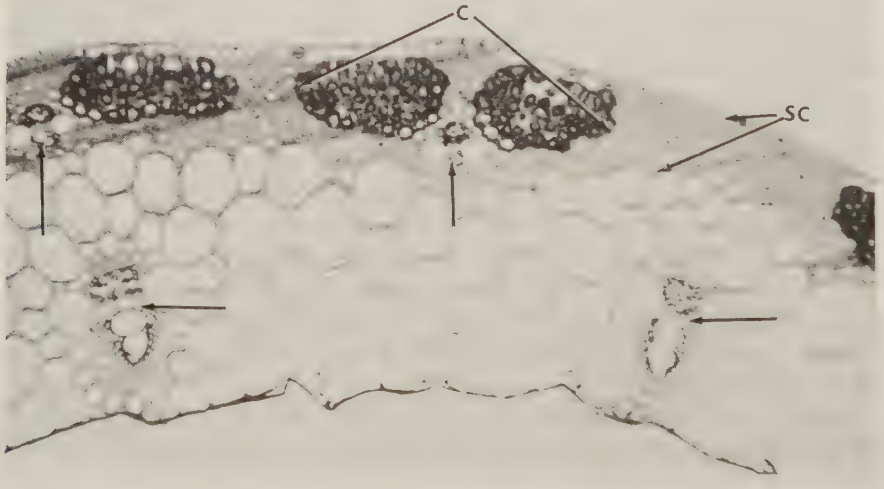

Fig. 2–9. Portion of stem cross-section. Hypodermal sclerenchyma sheath (*sc*) is interrupted at regular intervals by chlorenchyma strips (*c*), which are in turn bisected by the small bundles of the outer ring (*vertical arrows*) and their bundle sheath extension. Sclerified parenchyma extends from sclerenchyma to the hollow pith (*bottom of photo*). Large bundles of the inner ring (*horizontal arrows*) are embedded in this parenchyma. × 55.

bundles descend into the internode below; small ones become the outermost ring of small stem bundles while large ones turn inward, then descend as part of the inner ring of larger culm bundles. They alternate with bundles that descended from the inner ring of the internode above (Patrick, 1972a).

At each node, about half of the inner ring bundles from the internode above merge with other bundles, and all descending outer ring bundles turn inward to form the nodal plexus, a network of bundles connecting all incoming leaf bundles with all descending culm bundles (Patrick, 1972a). The outer internode ring is then replaced by incoming small longitudinal leaf bundles.

Every internode therefore has an outer ring of small bundles derived from the small longitudinal leaf bundles that entered the node immediately above, and an inner ring of large bundles variously derived from large longitudinal bundles of the three leaves above. At each node, all stem bundles and all incoming leaf bundles are interconnected by horizontal bundles in the nodal plexus (Fig. 2–10). This complex but repeating vascular pattern is typical of festucoid grasses (Hitch and Sharman, 1971).

Vascular bundles in leaves and in culm internodes are collateral, with an inner strand of xylem and an outer phloem strand, but where bundles merge in nodes they become amphivasal: i.e., phloem is surrounded by xylem for a short distance (Chrysler, 1906; O'Brien and Zee, 1971). O'Brien and Zee (1971) recognized three types of modified bundles, one with numerous xylem transfer cells but no phloem transfer cells in leaf bundles just entering the node, and two horizontally oriented types with phloem transfer cells but no xylem transfer cells. Xylem transfer cells may redirect solutes to young leaves from xylem strands that would otherwise transport solutes to mature leaves (Busby and O'Brien, 1979). They pointed out that there are no true stem bundles, only extensions of leaf bundles that stay in the culm for one to three internodes; thus, solutes must move from leaf bundle to leaf bundle at nodes as they flow upward. Xylem transfer cells have been verified by scanning electron microscopy (Chambers and Hamilton, 1973). The function of phloem transfer cells is unknown.

2–1.4 Mature Root

The anatomy of seminal roots of seedlings or aboveground portions of prop roots has been studied, but not subterranean roots of older plants. Prop roots are larger than seminal roots, have a sclerotic outer cortical zone, and possess chloroplasts in thin-walled cortical parenchyma cells (Percival, 1921).

The root cap is a mucilage-covered pad of parenchyma cells at the root tip (Fig. 2–11, 2–12). The gelatinous polysaccharide mucilage is secreted by superficial cells (Miki et al., 1980). Roots have a polyarch vas-

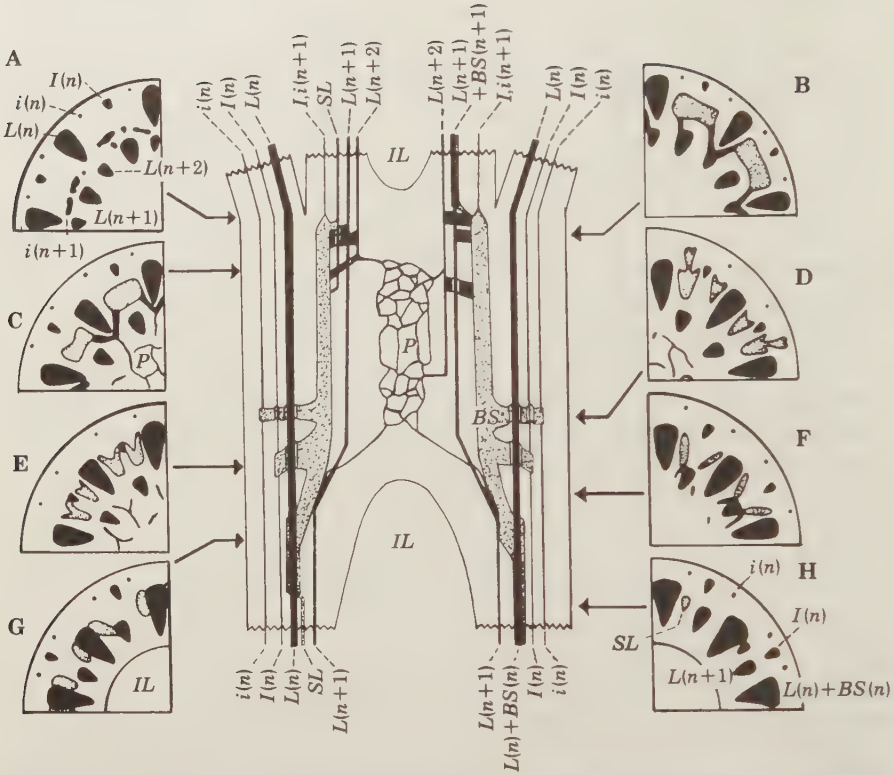

Fig. 2–10. Diagram showing vascular structure of a representative node in longitudinal and transverse views. *IL*, Internodal lacuna (hollow pith); *P* Pith plexus in nodal plate; *BS*, Bridging strands; *L*, Large bundle of leaf; *I*, Intermediate bundle of leaf; *i*, Smallest longitudinal bundle of leaf; *SL*, Subsidiary lateral bundle, a fusion bundle that will traverse internode below; *n*, bundle from leaf at this node; (*n*+*1*), Bundle from leaf one node above; (*n*+*2*), Bundle from leaf two nodes above. From Patrick (1972a), with permission.

cular pattern, with 7 to 11 protoxylem ridges. Small roots have a single large central metaxylem element (Fig. 2–13); larger roots have sclerified pith parenchyma. The phloem consists of slender strands of two to four sieve tube members between adjacent protoxylem ridges. Sparse phloem in roots is typical for annual species that store photosynthates mostly in reproductive structures, especially the endosperm of the seed. A single-layered pericycle just outside of the protoxylem and phloem strands delimits the central cylinder, also called the *stele*. Pericycle cells become sclerified in older parts of a root. The endodermis, a single layer of cells just external to the pericycle, is the innermost cortical layer. It has thickened inner tangential and radial walls and a thin outer tangential wall, a feature of unknown significance found in varying degrees among grasses.

Fig. 2–11. Root tip of maize with droplet of root cap mucilage. Arrowheads indicate tip of root proper meristem. Wheat roots are similar. From Miki et al. (1980), with permission.

2–2 VEGETATIVE DEVELOPMENT FROM THE GRAIN

2–2.1 Mature Grain

2–2.1.1 Pericarp and Seed Coat

The mature wheat seed is fused with its thin pericarp, or fruit coat, so seed and fruit form one unit, the caryopsis or grain (Fig. 2–14). Grain shape is affected by its position in the spike or spikelet, and by the amount of stored endosperm (plumpness); grains may be ovate, elliptical, or oval (Briggle and Reitz, 1963). On the ventral face of the grain is the crease, in which there is a single vascular bundle with an accompanying parallel strand of crushed cells (pigment strand) whose walls are coated by polyphenolic and lipoidal substances (Fig. 2–15).

The pericarp usually has a tuft of hairs (brush) at its stigmatic end and an attachment scar at the opposite end (Fig. 2–14). Grains are reddish brown, amber (yellow), white, or intermediate hues depending on endosperm texture; for example, hard-textured (vitreous) red and amber grains appear darker in color than soft-textured (starchy) white grains.

The pericarp, except in the crease, is five or six cell layers thick (Percival, 1921). The epidermis and the underlying one- or two-layered hypodermis make up the outer pericarp (Fig. 2–16, no 4). The cells are closely packed and elongated parallel to the grain axis. Functional stomata, 16 to 25 per grain, are distributed along the crease near the brush. They may be part of a transpiration-driven mechanism that moves assimilates into the developing grain (Lee and Atkey, 1984). The inner

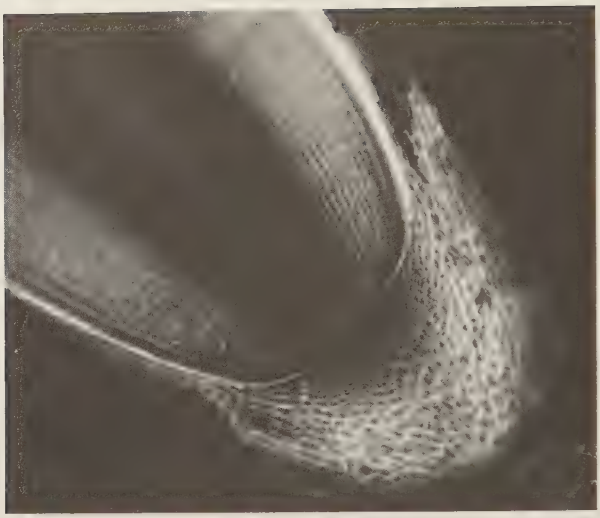

Fig. 2–12. Longisection of fresh maize root tip. Autofluorescing mucilage can be seen in root cap and strongly over epidermis of root proper. Wheat roots are similar. From Miki et al. (1980), with permission.

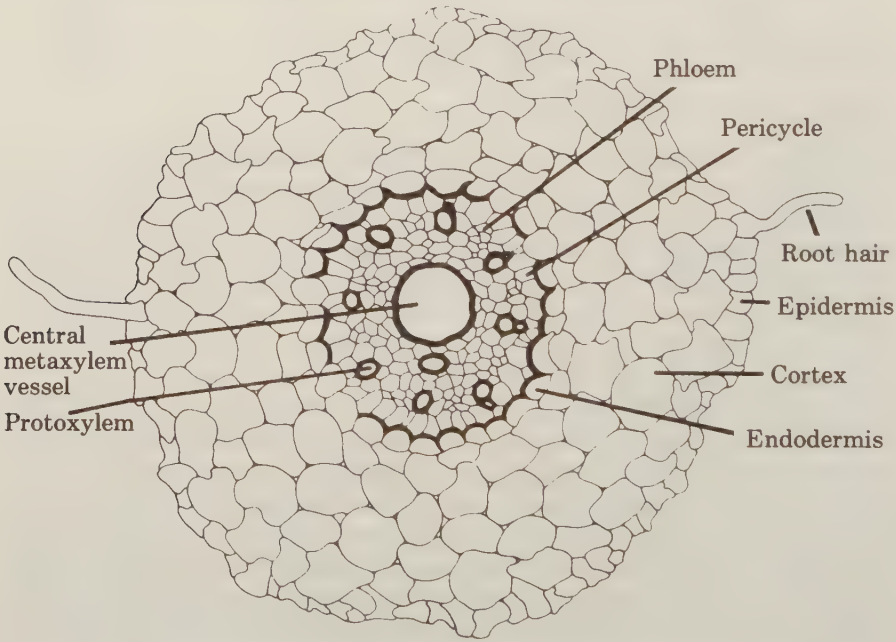

Fig. 2–13. Cross-section of seedling root. From Fahn (1982), with permission. × 120.

pericarp is made up of thin-walled intermediate cells and underlying cross and tube cell layers (Fig. 2–16, no. 4). Elongate, sclerified cross cells form a tight layer with cell axes perpendicular to the grain axis. The underlying

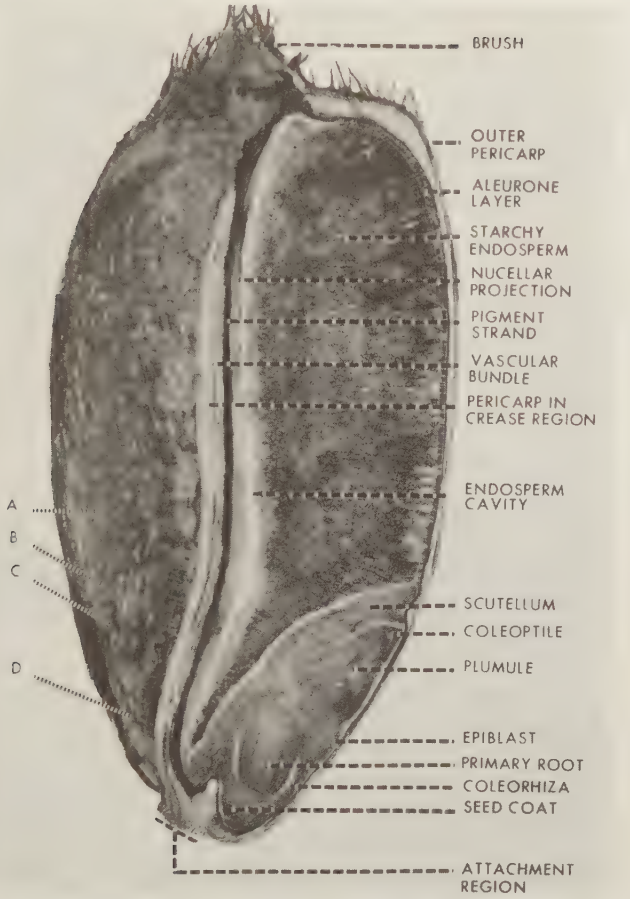

Fig. 2–14. The wheat kernel in cutaway longitudinal view. Courtesy of Northern Utilization and Development Division, USDA-ARS. ca. × 20.

tube cells are longer and thinner, and are isolated or only infrequently touching each other, with extensive intercellular spaces.

Beneath the pericarp is the scanty seed coat, which consists of only a thin layer of crushed cells (Fig. 2–16, no. 4) in which an outer and inner cuticle with a pigmented color layer in between may be detected (Bradbury et al., 1956a). The nucellus has only one or two cell layers (Fig. 2–16) or is merely a hyaline layer. The nucellar projection (Fig. 2–15) is a cellular band occurring parallel to the pigment strand.

2–2.1.2 Endosperm

Endosperm is the starchy tissue that forms during grain development. It provides nourishment for the developing embryo, and for the seedling after germination until it can establish itself. Endosperm is also the major

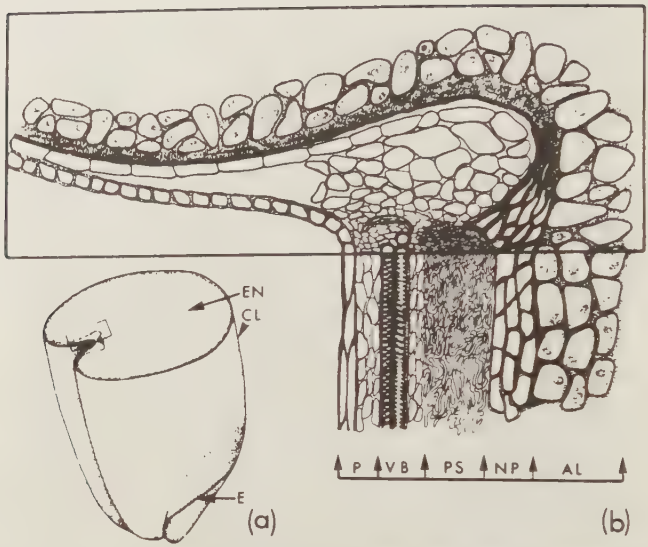

Fig. 2–15. Crease region of the grain. (*a*), Grain with distal half removed; *E*, Embryo; EN, endosperm; *CL*, Covering layers. Rectangle indicates area of crease shown in detail in (*b*). *AL*, Aleurone layer; *NP*, Nucellar projection; *P*, Pericarp; *PS*, Pigment strand; *VB*, Vascular bundle. From Zee and O'Brien (1970), with permission.

reason why wheat and other cereal grain grasses are cultivated; flour is made from this tissue.

Endosperm occupies about 90% of the mature grain's interior, except where it is displaced by the embryo (Fig. 2–14), and it accounts for 90% of the total weight of the grain. The endosperm is bounded externally by the aleurone layer, which consists of blocky to somewhat radially elongate cells in contact with the nucellar remnant (Fig. 2–14 and 2–16, no.4). The thick aleurone cell wall has two layers distinguishable by differential staining or by transmission electron microscopy (Bacic and Stone, 1981; Fulcher et al., 1972a; Morrison et al., 1975). Aleurone cytoplasm lacks starch but is rich in protein granules (aleurone grains) that are each surrounded by lipid droplets. Cytohistological staining shows that aleurone protein has three times more arginine than starchy endosperm protein (Fulcher et al., 1972b). Nuclear chromatin is strongly aggregated in aleurone cells, and dictyosomes are difficult to identify, but other organelles and lipid and protein bodies are well defined (Swift and O'Brien, 1972a). Aleurone cells remain alive in mature grains (Bradbury et al., 1956b).

Starchy endosperm fills most of the grain (Fig. 2–14). Its cells are dead at maturity but packed with starch and matrix protein (Campbell et al., 1981). These workers verified that there is a decreasing protein gradient from the aleurone layer to the center of the starchy endosperm.

2–2.1.3 Embryo

The embryo is an immature new plant (sporophyte) that is arrested in a dormant state in the seed. Dormancy is mostly the result of gradual

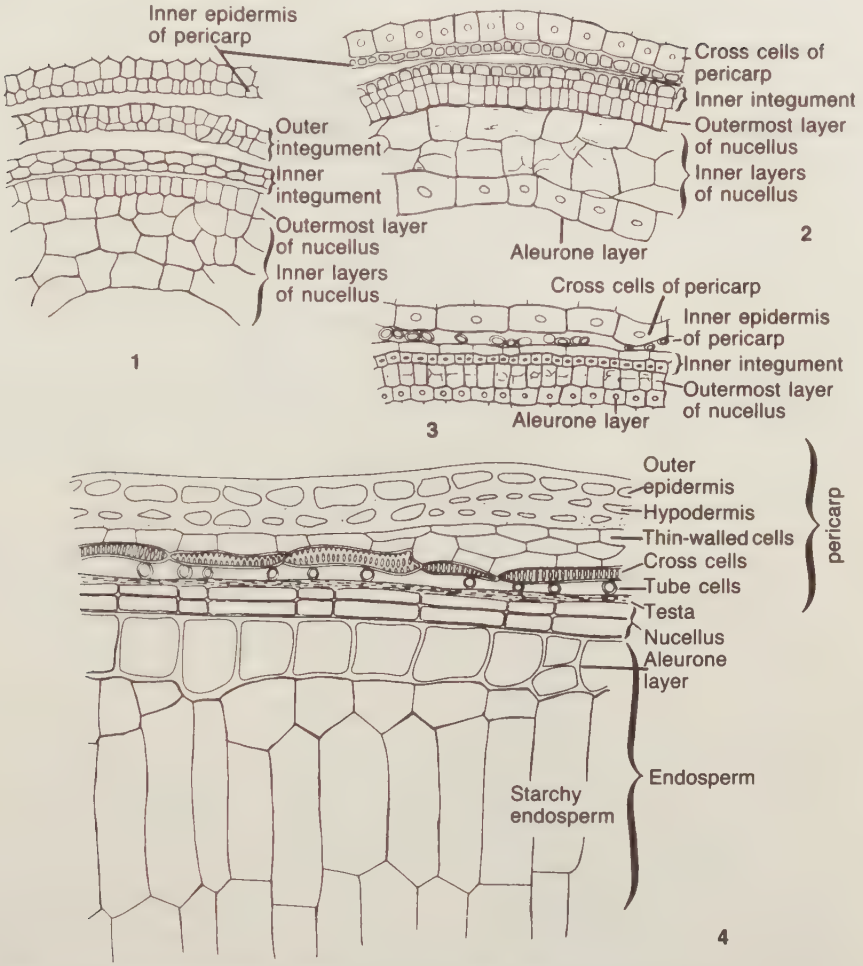

Fig. 2–16. Pericarp, seed coat, nucellus, and aleurone layer in the developing (*1–3*) to mature (*4*) caryopsis. From Fahn (1982), with permission. ca. × 200.

drying out of all grain tissues, but in some plants chemical inhibitors produced by the endosperm have also been identified as a dormancy-inducing factor.

The relatively small wheat embryo is appressed to the seed coat (Fig. 2–14 and 2–17a). Roughly circular as seen from front or back (Fig. 2–17b), in median longitudinal section it appears as a tubular embryo axis from which protrudes a thick, disclike scutellum (Fig. 2–14 and 2–18).

The scutellum, often interpreted as the single cotyledon (Brown, 1960, 1965), has a palisade epithelial epidermis (Fig. 2–18 and 2–20) with organelles and membranes intact (Swift and O'Brien, 1972a). It is vasculated in an unusual way. A single *scutellar trace* extends from the coty-

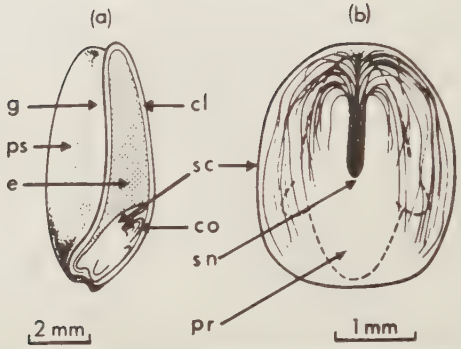

Fig. 2–17. *a*, Sagittal section of grain; *b*, Diagrammatic dorsal view of scutellum, as seen from endosperm. Fine lines arching upward, then down, are scutellar vascular strands. Embryo axis, indicated by dotted lines, is behind scutellum, with pair of lateral seminal roots. *Cl*, Covering layers (aleurone through pericarp); *Co*, Coleoptile; *E*, Endosperm; *g*, Groove (crease); *pr*, Primary root; *ps*, Pericarp surface; *sc*, Scutellum; *sn*, Scutellar node. From Swift and O'Brien (1970), with permission.

ledonary node to near the scutellar apex (Fig. 2–18), where it diverges into numerous slender procambial strands that arch back downward. These strands end at various levels, but none extends to the scutellar base (Fig. 2–17b). When mapped in detail (Swift and O'Brien, 1970), most of the strands in this vascular array were found to lie near the epithelium.

During germination, the scutellum performs three tasks: (i) it secretes a hormonal message to the aleurone layer, (ii) it secretes hydrolytic enzymes, and (iii) it regulates endosperm mobilization (Negbi, 1984).

The conical coleoptile of the embryo is often regarded as the first leaf, or prophyll (Brown, 1960). It has a subapical slit facing away from the scutellum. Fahn (1982) (Fig. 2–18) shows three or four layers of mesophyll in the scutellum, but a more detailed description shows two ascending vascular bundles, one on each side, which merge at the tip (O'Brien and Thimann, 1965; Thimann and O'Brien, 1965). Two rows of stomata in the outer epidermis flank each bundle. The guard cells, surprisingly, are not linear, as is usual in grasses, but instead are bean-shaped, as in other families. Stomata are infrequent on the inner epidermis. Outer epidermal cell walls are thickened irregularly, possibly an adaptation to protect the delicate plumule as the coleoptile pushes through the soil during germination.

The coleoptile usually encloses three immature leaves, the shoot apex, and an axillary bud (Fig. 2–18). A small nonvasculated flap (epiblast) arises from the embryo axis on the side opposite the scutellar attachment.

The lower part of the embryo consists of the relatively massive primary root (radicle) enclosed by the coleorhiza (Fig. 2–18), which is a sheath-like structure bearing the suspensor remnant. The coleorhiza has been interpreted as the aborted primary root, and the primary root as the first adventitious root (Brown, 1960). Two pairs of adventitious seminal roots (Fig. 2–19) are also present. Virtually all vascular tissue is still undifferentiated procambium in the mature embryo.

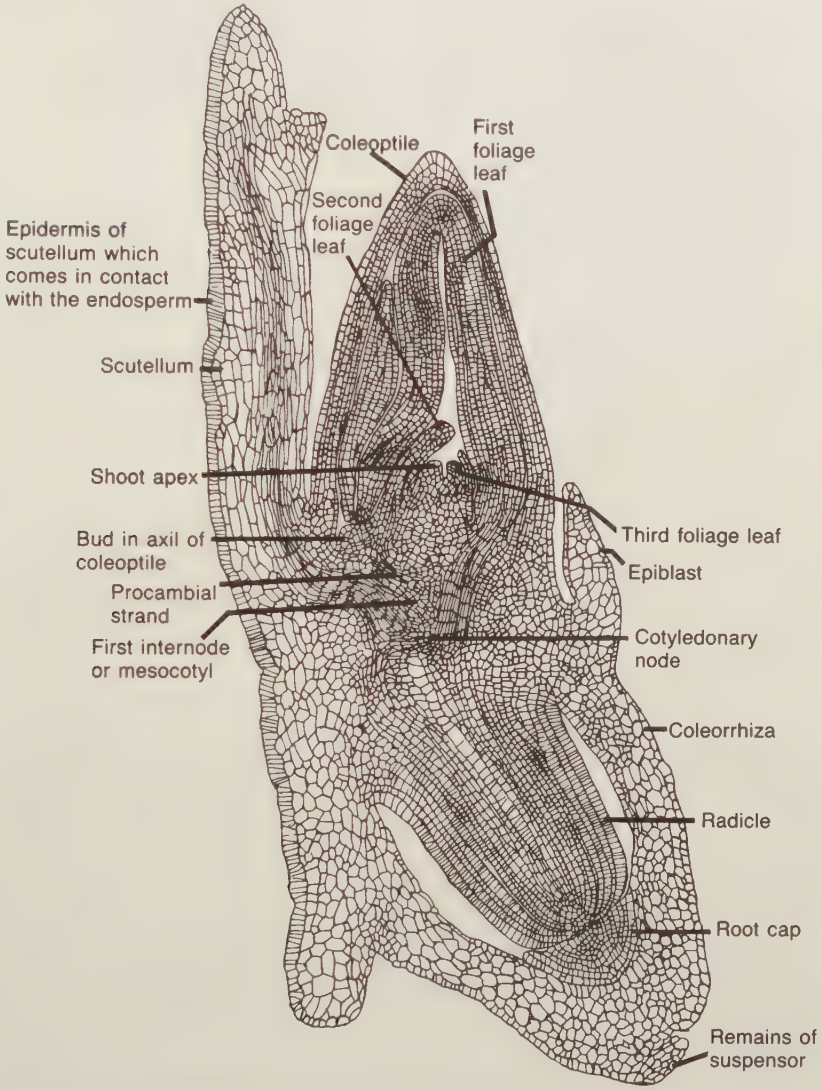

Fig. 2–18. Median longisection of mature embryo. From Fahn (1982), with permission. ca. × 50.

The embryo contains oil and protein but little starch. Because oil can become rancid, the embryo usually is separated from endosperm before flour milling (Bradbury et al., 1956c).

2–2.2 Germination and Seedling Growth

2–2.2.1 Endosperm Digestion

For germination to begin, water and oxygen must enter and permeate the grain. In wheat, several pathways for water entry have been proposed

Fig. 2–19. Frontal section of embryo 15 to 20 days old, to emphasize lateral root primordia (*lrp*). Bar = 100 μm. Rogers and Quatrano (1983), with permission.

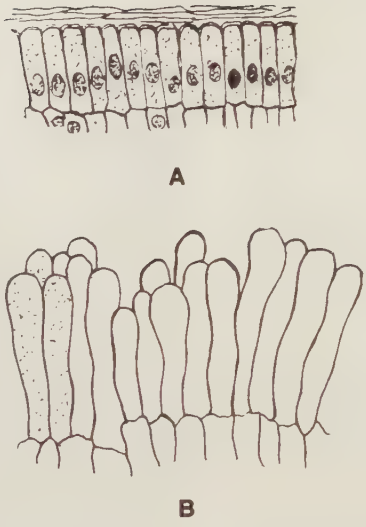

Fig. 2–20. Epithelium of scutellum. *A*, In dormant embryo. *B*, Elongated and partly separated epithelial cells in germinating embryo. From Percival (1921). ca. × 250.

(Bradbury et al., 1956c). There is evidence that water follows the pigment strand in the crease to the endosperm and, from there, to the embryo and the aleurone layer (Zee and O'Brien, 1970). Upon activation by water with its dissolved oxygen, the scutellum secretes gibberellic acid, which in turn stimulates the aleurone cells to secrete enzymes that degrade proteins and digest starch (Smart and O'Brien, 1979a).

Upon hydration of the scutellum, its epidermal cells (Fig. 2–18) elongate from 40 to 80 μm (Percival, 1921) and separate (Fig. 2–20). Within the scutellum, protein bodies are degraded, phytin disappears, and starch accumulates (Smart and O'Brien, 1979a; Swift and O'Brien, 1972b). The starch forms first in basal scutellar cells, gradually reaching the apex by the 3rd day. Protein and phytin disappear first in the apex, the reverse of starch accumulation, and by the 7th day they are both gone from the scutellum. The scutellum therefore mobilizes its own reserves first, for early embryo growth, then provides temporary storage of endosperm starch for continued embryo development. Although the scutellar epithelium both secretes and absorbs, its cells lack the typical subcellular appearance of secretory cells (Swift and O'Brien, 1972b).

As these changes occur, scutellar procambium (Fig. 2–17b) begins to differentiate into xylem and phloem. Many vascular strands in the scutellum, or at least their distal parts, consist only of sieve tubes surrounded by parenchyma (Swift and O'Brien, 1970). This spray of slender phloem strands occurs mostly near the epithelium, which lies against the endo-

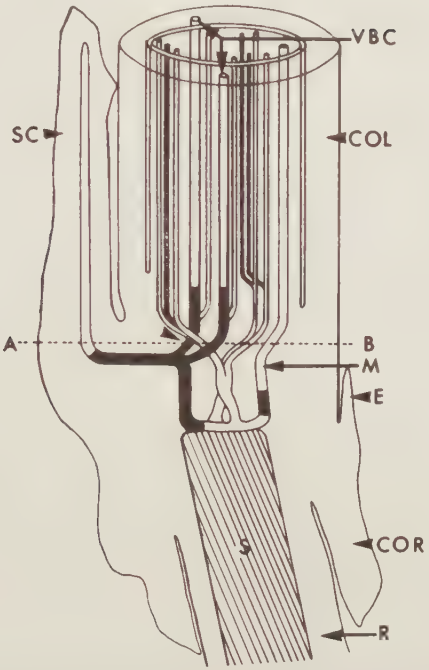

Fig. 2–21. Diagram of part of seedling showing vascular interconnections. The two transfer cell zones are in solid black. Dotted bundles are the midvein and two lateral longitudinal bundles of the second foliage leaf. Open bundles are the midvein and six lateral bundles of the first foliage leaf. Line A–B and arrowhead can be ignored. *COL*, Coleoptile; *COR*, Coleorhiza; *E*, Epiblast; *M*, Midvein of first foliage leaf; *R*, Radicle; *S*, Stele of radicle; *SC*, Scutellum; *VBC*, Bundles of coleoptile. From O'Brien et al. (1970), with permission.

sperm; this specialized vasculature is thus well positioned to transport the products of starch digestion into the embryo axis.

How does the scutellum secrete enzymes that can degrade endosperm cell walls without also dissolving its own epidermal cell walls? Omitting details, scutellar epidermal cell walls have two layers that stain differently from endosperm walls. Similar layers make up the aleurone cell wall, suggesting that such a wall composition allows both the scutellum and the aleurone layer to resist enzyme degradation (Smart and O'Brien, 1979b).

Endosperm starch grains near the scutellar apex become cracked and pitted on the 2nd or 3rd day of germination. This visible evidence of starch digestion spreads gradually to the grain apex, then around the flanks beneath the aleurone layer. Further digestion is from the outside toward the center (Percival, 1921).

2-2.2.2 Embryo Growth

As digested endosperm is absorbed by the scutellum, nutrients are conveyed through it and the embryo axis will elongate and begin to

differentiate. These processes accelerate after functional vascular connections are established between the scutellum and the embryo axis about 18 h after germination. Phloem differentiation spreads from four loci, whereas tracheary elements differentiate from just two loci, and they lag behind the phloem (Swift and O'Brien, 1971).

Transfer cells develop in two places in the embryo axis. These parenchyma cells, with wall ingrowths that greatly increase their outer cell membrane area, are restricted to xylem parenchyma cells in the horizontal extension of the main scutellar bundle in the coleoptilar node (Fig. 2–21) and a smaller nearby area of the bundle that extends upward to become the midvein of the first foliage leaf (O'Brien et al., 1970). The transfer cells may remove organic N from the xylem and shunt it to nearby phloem for transport to developing roots and plumule (O'Brien et al., 1970).

After the isolated patches of differentiating vascular tissue have linked up, the embryo starts to expand. The coleorhiza dilates, rupturing its covering layers and exposing the embryo axis. The growing primary root soon pierces the coleorhiza, which may form its own root hair–like epidermal protuberances (Percival, 1921). The first pair of lateral adventitious roots grows out soon after.

The plumule grows within the elongating coleoptile, which reaches about 5 cm in length (Thimann and O'Brien, 1965). Coleoptile vascular bundles differentiate from the base toward the tip. Later, as intercalary meristem activity ruptures existing vascular cells at the base of the coleoptile, they are replaced with new ones. Stomata differentiate from tip to base. When the coleoptile stops elongating, the developing shoot within it pushes through the slit.

Seedling vascular architecture, as in the mature plant, is complex (Fig. 2–21). Primary root vasculature is connected to that of the rest of the seedling at the cotyledonary node. The first internode is also where the vascular bundles are in transition to the vascular pattern described previously for the mature culm (section 2–1.3).

2–2.3 Primary Meristems and Organ Differentiation

2–2.3.1 Stem Apical Meristem

Following germination, the shoot apex changes in size and shape from seedling to adult. Just after germination there is a single outer tunica layer over a small inner corpus of isodiametric cells (Opatrna et al., 1964). Later, as foliage leaves are initiated, peripheral corpus cells form a hypodermal layer that resembles a second tunica layer (Fig. 2–22).

2–2.3.2 Leaf Development

Each leaf primordium arises on the flank of the tall shoot apex as a horizontal ridge that expands laterally both ways until it has more than encircled the node. Its edges therefore become slightly displaced and

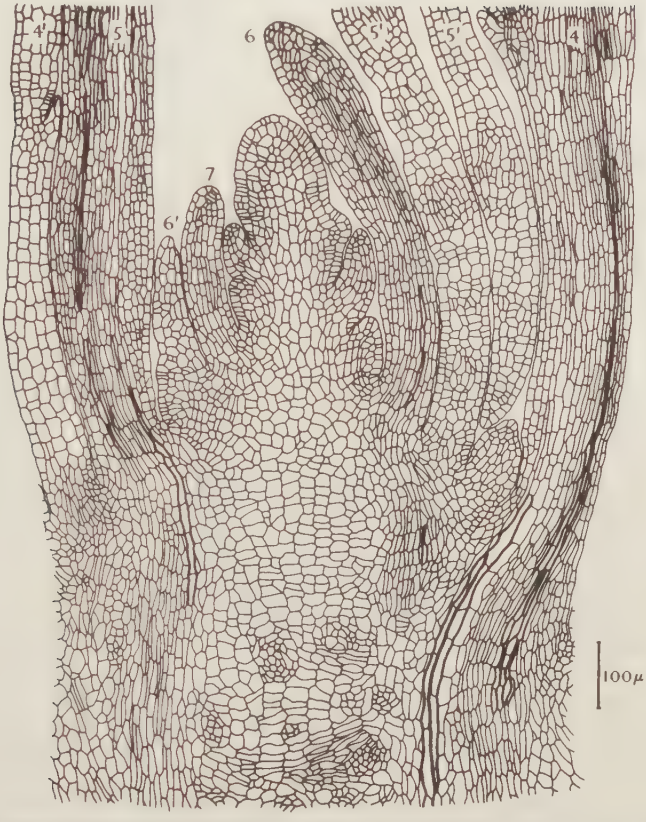

Fig. 2–22. Radial longitudinal section of shoot tip, cut in the plane of the leaves. *4–6*, Midregion of base of leaf. *4'–6'*, Encircling portion of leaves 4 to 6; *7*. Leaf primordium 7. Isolated linear strands of differentiated tracheary elements can be seen. From Sharman and Hitch (1967), with permission.

overlapping (Fig. 2–23 and 2–25) (Williams, 1975). The sheathlike leaf grows upward as a conical cap over the shoot apex and younger leaves developing within (Fig. 2–23).

Within an individual developing leaf, the procambium that will differentiate into the longitudinal bundles is initiated as isolated strands. Midvein procambium appears first at the base of the leaf, then it extends upward into the leaf and downward into the node (Fig. 2–22 and 2–24). Other longitudinal bundles are initated later but they differentiate similarly (Sharman and Hitch, 1967). Cross veins appear after longitudinal bundles have started to differentiate into protophloem and protoxylem, maturing first at the tip, then progressively toward the leaf base (Blackman, 1971; Patrick, 1972b).

The behavior of meristems within the leaf, or differentiation of leaf tissues other than vascular tissues, seems unknown except for a study of stomatal apparatus formation. Pickett-Heaps and Northcote (1966) reported that an initial asymmetrical protodermal cell division forms a

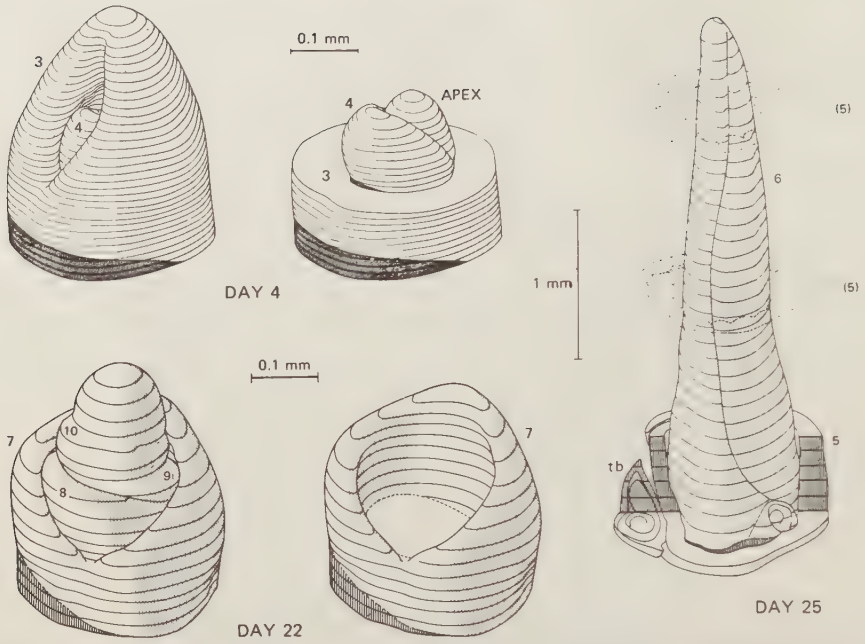

Fig. 2–23. Reconstruction of shoot apex and leaf primordia at given days after germination. *Day 4*, (*left*) leaves 3 and 4 cover apex; (*right*) leaf 3 is removed to show apex. *Day 22*, (*left*), apex and primordia 7 to 10 (older leaf 6 removed); (*right*), only leaf 7 is shown. *Day 25*, leaf 6 completely encloses leaves 7 to 10 and apex. Dotted lines indicate older, enclosing leaf 5. Tiller bud (*tb*) is present. From Williams (1975), with permission.

guard mother cell. Symmetrical divisions in neighboring cells produce subsidiary cells. Finally, a symmetrical guard mother cell division forms the two guard cells.

2–2.3.3 Tiller Growth

Tiller initiation and growth has been studied in great detail (Williams et al., 1975). Buds form in the axils of most leaves. Each bud develops a prophyll (first leaf) similar to the coleoptile (Fig. 2–25). Tiller buds become squeezed and flattened by pressure from the tightly wrapped developing leaf bases (Fig. 2–23). Tiller buds make early vascular connections with the adjacent nodal plexus and bundles descending from higher leaves. Tillers are therefore connected to the entire vascular system of the main axis.

About eight buds will form, but only three or four develop into full-size tillers. Physical constraint of tiller buds by surrounding leaf sheaths may be a factor in determining the tillering pattern, in combination with external factors such as variation in light intensity, temperature, and N levels (Williams et al., 1975).

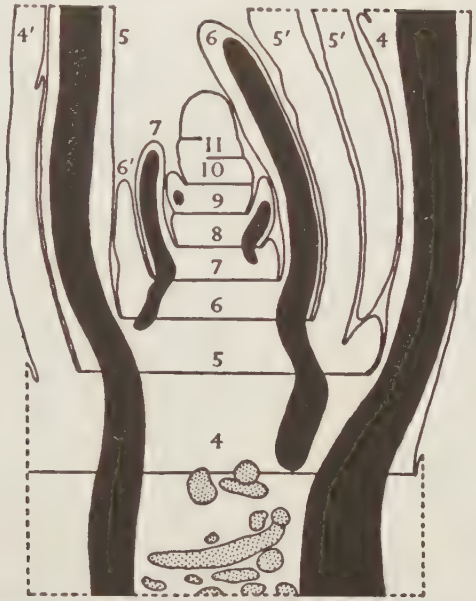

Fig. 2–24. Interpretive diagram of Fig. 2–22, showing isolated procambial strand initiation and differentiation (*thick black lines*) in midvein of developing leaves. From Sharman and Hitch (1967), with permission.

2-2.3.4 Root Growth

Grasses are among a small number of families in which the root cap has its own initials, so the cap is sharply distinct from the rest of the root (Fig. 2–13 and 2–26). The root proper has a subapical meristem (Clowes, 1961) in which a central cluster of cells (the irregular, semicircular zone just above the root cap in Fig. 2–26b) has an extremely low rate of division. This common feature in plants has been described in detail for wheat by Hejnowicz (1959), who named it the *inactive center.* It is now more commonly called the *quiescent center* (Clowes, 1961).

The tipmost 4.5 mm of each wheat root is the zone of growth, and mitoses are rather uniformly distributed in the distal 2.0 mm except for the quiescent center (Hejnowicz, 1959). The epidermis/cortex arises from peripheral cells of the subapical meristem, whereas the central vascular cylinder arises from a central portion (Fig. 2–26). Differentiation occurs gradually away from the meristem.

The root epidermis, which is palisadelike near its tip, secretes a firmer mucilage than the root cap (Fig. 2–12). Two chemically different layers have been detected (Miki et al., 1980). Phenolic substances in the outer layer may protect against certain pathogens in the soil.

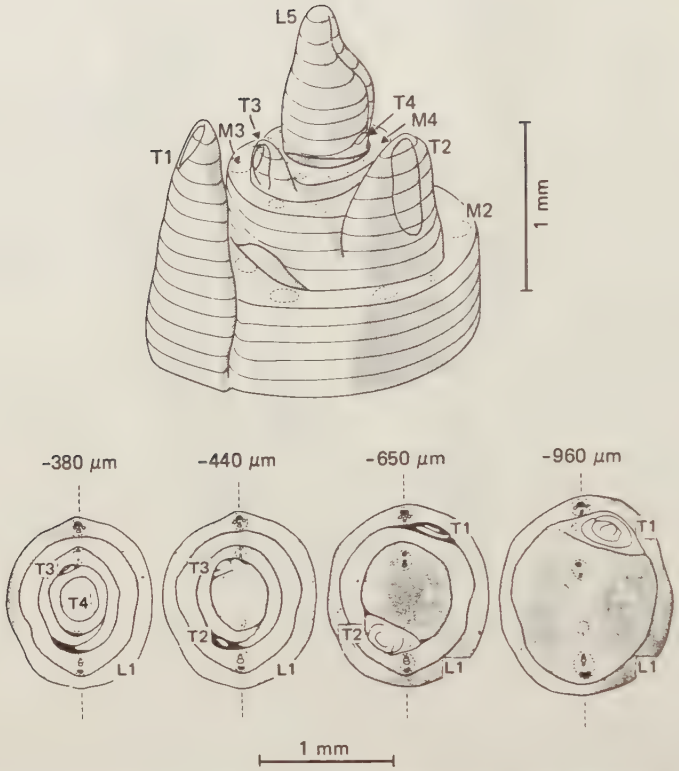

Fig. 2–25. Above, reconstruction of the subapical region of a 17-day shoot tip. Leaves 1 to 4 are removed to expose their respective tiller buds (*T1–T4*). Note that tiller buds are offset from the midvein (*M2–M4*) of the subtending leaf. Leaf 5 (*L5*) covers the shoot apex. Below, outlines of transverse sections through a shoot tip similar to that reconstructed above. Distances below the shoot apical dome are indicated for each section. Tightly wrapped, overlapping leaves and offset tiller buds are evident. From Williams et al. (1975), with permission.

Epidermal cells gradually become flat and tabular and cease to secrete mucilage as the root elongates within the first 2 mm behind the root tip (Miki et al., 1980). Some epidermal cells then generate root hairs, 170 to 350 μm in length, which greatly increases the absorbing surface area. The short-lived root hairs probably exist for 1 to 3 weeks, and are replaced at about the same rate that they die off, so root hairs are maintained as an almost constant zone near the root tip.

Lateral (branch) roots are initiated in the pericycle (Fig. 2–13), opposite a phloem strand and between two protoxylem ridges. These proliferating pericycle cells later form a typical root organization, make vascular connections with the parent root, and eventually grow through the cortex and epidermis of the parent root to emerge into the soil. It is not clear where and how adventitious roots are initiated and develop, except that they arise from culm nodes (Percival, 1921).

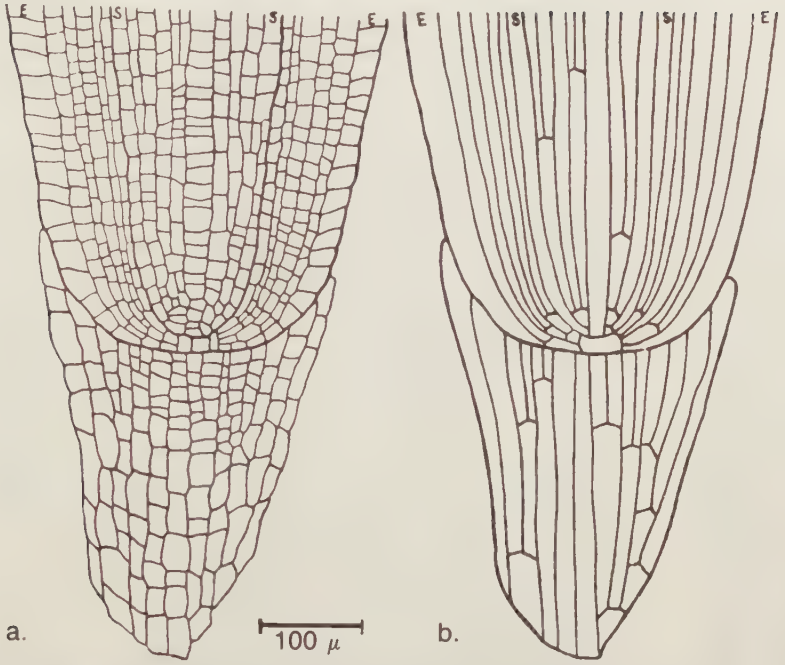

Fig. 2–26. Median longitudinal section of wheat root tip showing cellular structure (*a*) and Korper-Kappe pattern of cell division trends (*b*). Root cap is clearly distinct from root proper. Irregular zone at tip of root proper is the quiescent center. *E*, Epidermis; *S*, Delimiting layer of stele. From F.A.L. Clowes, (1961), Apical meristems, Blackwell's Scientific Publishers, with permission.

2–3 REPRODUCTION

2–3.1 Inflorescence

Each tiller apex eventually stops producing leaves, becomes greatly elongated, and then forms bracts and axillary spikelets (Opatrna et al., 1964). Early stages of inflorescence development have been described in great detail, as well as cellular events in abnormal inflorescences affected by 2, 4-D treatment (Sharman, 1983).

The inflorescence is a spike (Fig. 2–27, nos. 1 and 2) with a main axis (rachis) bearing spikelets separated by short internodes. Each spikelet is a condensed reproductive shoot (Fig. 2–27, no. 3) consisting of two subtending sterile bracts (glumes) (Fig. 2–27, nos. 4 and 5) enclosing two to five florets (Fig. 2–27, nos. 6–10, Fig. 2–28), all borne distichously (double-ranked) on a short axis (rachilla). Each floret is enclosed by two bractlike structures, the lemma (Fig. 2–27, no. 13) and the palea (Fig. 2–27, no. 14). Within each floret are three stamens (Fig. 2–27, no. 16) with large anthers (Fig. 2–27, no. 19) and a pistil (Fig. 2–27, nos. 17, 20–22) bearing two styles with feathery stigma branches (Fig. 2–27, nos. 23 and 24). There are also two ovate lodicules (Fig. 2–27, no 15), which are

Fig. 2–27. Wheat inflorescence, spikelet, and pollination. *1*, Spike, dorsiventral view; *2*, Spike, lateral view; *3*, Spikelet on naked rachis; *4*, Upper glume; *5*, Lower glume; *6–10*, Progressively smaller florets of a spikelet; *11*, Floret anthesis in lateral view; *12*, Glume; *13*, Lemma; *14*, Palea; *15*, Lodicules; *16*, Unopened floret showing stamens (*s*) and pistil (*t*), and outline of palea and lemma (*x*); *17*, Floret at anthesis with pistil (*u*) and elongating stamen filaments; *18*, Floret cross-section showing positions of palea (*c*), lemma (*k*), stamen (*v*), and stigma (*w*); *19*, Anther cross-section showing four locules and central connective; *20–22*, Appearance of pistil before, during, and after anthesis; *23*, Pollen on stigma branches; *24*, Pollen germinating on stigma branch; *25*, Spherical pollen grains. Each has one pore (not shown); *26–32*, Florets from before to after anthesis (26 to 31 take 2 to 5 min, 31 to 32 take 20 to 35 min).

interpreted as highly modified perianth structures. Lodicules are vasculated solely by phloem strands, with associated transfer cells at their base (Zee and O'Brien, 1971b).

Transfer cells also occur in the nodal vascular plexus where the rachilla joins the rachis, and in the rachilla where glumes, lemma, palea, and pistil are attached. Anatomical evidence and tracer experiments indicate that these transfer cells help to regulate solute flow into the developing caryopsis (Zee and O'Brien, 1971a).

Fig. 2–28. Partly dissected wheat spike showing interior of one floret at center.

2–3.2 Stamen and Pollen

Wheat stamens are smaller, and produce fewer pollen grains (1000 to 3800 per anther) than other cereal grasses. Only about 450 000 are produced per plant as compared, for example, to about 4 million and 18 million for rye (*Secale cereale* L.) and maize, respectively (Vries, 1971).

Four cylindrical columns of microspore mother cells form, one in each lobe of the young anther (Fig. 2–27, nos. 18 and 19). Each of these columns is surrounded by a single-layered tapetum, a nutritive layer that performs multiple and still not completely known functions during pollen development. Outward from the tapetum are the middle layer, endothecium, and epidermis (Fig. 2–29, no. 1). The central cylinder of the anther, called the *connective*, consists of parenchyma surrounding a single central vascular bundle. Each microspore mother cell deposits a thin layer of a carbohydrate called *callose* (a β-1-3 glucan) around itself and into the center of the locule (McQuade and Pickles, 1980). Callose seems to be a firmly gelatinous substance that isolates each meiocyte from outside influences during its meiotic shift from sporophyte to gametophyte generation.

Meiosis in microspore mother cells takes about 24 h (Bennett et al., 1971), with a cell plate formed after each division. The resulting tetrad, shaped rather like a pie cut into four pieces, is appressed to the tapetum

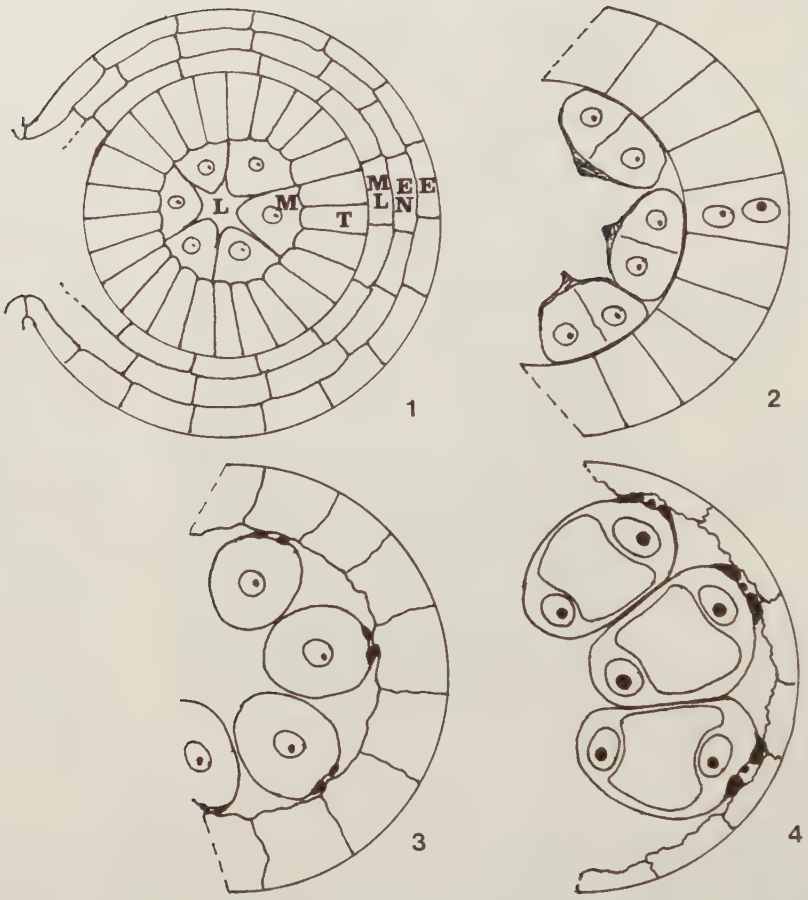

Fig. 2–29. Some stages of pollen development shown diagrammatically. *1*, Premeiosis; *L*, Locule; *M*, microspore mother cells; *T*, Tapetal cell layer; *ML*, Middle layer; *EN*, Endothecium; *E*, Epidermis. *2*, Tetrads of microspores appressed to binucleate tapetum. Two microspores in each tetrad are out of plane but also appressed. *3*, Microspores appressed to tapetum. Pore in microspore wall is at point of contact. *4*, Binucleate pollen grains, with vacuole, connected to collapsing tapetum by pollen wall pore.

(Fig. 2–29, no. 2). During meiosis, tapetal nuclei divide mitotically so that tapetal cells become binucleate (Fig. 2–29, no. 2), probably a sign of their increased metabolic activity.

The callose dissolves at some time after meiosis, but all microspores remain appressed to the tapetum until pollen is mature, and each forms a single pore at the point of tapetal contact (Fig. 2–29, no. 3). Such continued physical contact of developing pollen with the tapetum has so far been found only in grasses, where it is the rule (Christensen and Horner, 1974). A vacuole forms in each enlarging microspore, and each gradually constructs a complex pollen wall. Simply described, this wall consists of an outer, sculptured layer, the *exine*, mostly made of sporo-

pollenin, a tough carotenoid substance, and an inner layer, the *intine*, composed of cellulose. The single pore is the area where exine does not form, so that the intine is exposed here.

A nuclear division produces a two-celled structure, which can now be called the *pollen grain* (Fig. 2–29, no. 4), and which is still connected by its pore to the now collapsing tapetum. Food reserves gradually fill the pollen grain but, before the vacuole is filled with reserves, one nucleus divides again to form two lenticular, thin-walled cells, the sperm cells. Wheat pollen, as in other grasses, is shed in this three-celled condition.

A quantitative light microscope study of anther and pollen development contains more detailed information about these events (Bennett et al., 1973). Electron microscope details of the pollen wall are in Hu et al. (1979).

2–3.3 Carpel and Ovule

The unilocular carpel of wheat, as in other grasses, has one ovule and two plumose styles with stigma branches. The ovule bends approximately 90° and the two integuments grow asymmetrically (Aziz, 1972; Batygina, 1971) (Fig. 2–30). There are four ovary bundles: a short dorsal one, two lateral bundles that continue into the style branches, and a ventral ovule bundle (Fig. 2–31). A row of tabular cells extends from the ovule bundle to the enlarged hypodermal ovule cell that becomes the megaspore mother cell (Fig. 2–30, 2–32E). These tabular cells may be a kind of conducting tissue, and at megagametophyte maturity they may act as a hypostase (Batygina, 1971).

Two hypodermal cells in the ovule may enlarge (Fig. 2–32A), but only one will become the megaspore mother cell (Fig. 2–30 and 2–32B–E). This cell enlarges further and secretes callose around itself similar to the callose around microspore mother cells (Batygina, 1971; Bennett et al., 1973). Meiosis in the megaspore mother cell is synchronous with meiosis in the microspore mother cells; the process requires about 24 h in both places (Bennett et al., 1973).

Meiosis usually produces a linear tetrad of haploid megaspores (Fig. 2–32F–H), but T-shaped tetrads sometimes occur (Batygina, 1971; Bennett et al., 1973; Deshpande and Raju, 1979). Callose disappears from around the deepest-lying (chalazal) megaspore and, as in most other angiosperms, this cell enlarges to become the functional megaspore while the other three degenerate.

The functional megaspore develops into the megagemetophyte, more commonly called the *embryo sac*, by the typical (*Polygonum*) pattern that occurs in most angiosperms (Bennett et al., 1973; Deshpande and Raju, 1979). Three cycles of nuclear division produce eight nuclei within the now greatly enlarged megaspore (Fig. 2–32I, J). Three micropylar nuclei become surrounded by walls, forming an egg apparatus consisting of egg cell and two synergids. One nucleus from each pole migrates medianly to become the polar nuclei. They are the nuclei of the large central cell,

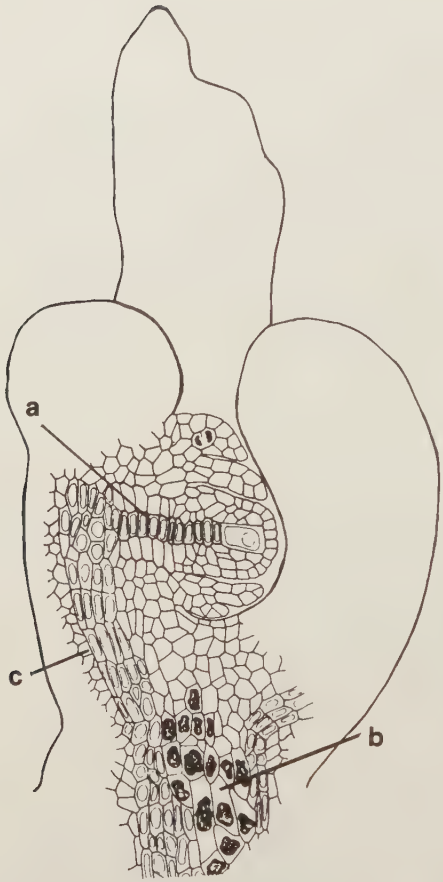

Fig. 2–30. Median longisection of ovary. Ovule has hypodermal megaspore mother cell with row of tabular cells (*a*) connecting it to procambium of ovular vascular bundle (*c*). integuments are developing asymmetrically. From Batygina (1971), with permission.

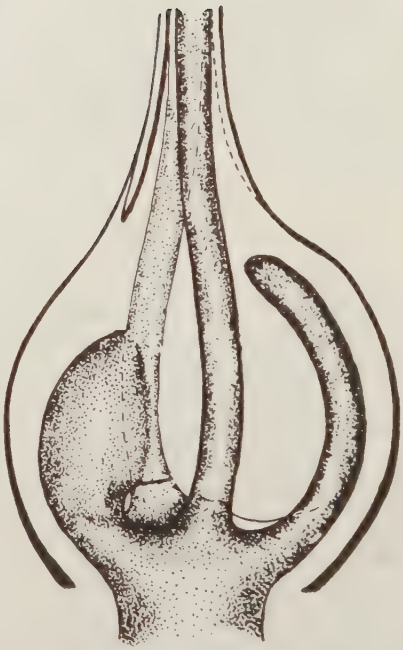

Fig. 2–31. Reconstruction of wheat ovary to show its vasculature. Short dorsal bundle at right ends near tip of ovary. Two lateral bundles extend into the style, and a short, thick bundle at left supplies the ovule (not shown). From Batygina (1971), with permission.

destined to become the endosperm later. The three chalazal nuclei also become cellular and, as is common among grasses, they proliferate further into 20 to 30 polyploid cells (Bennett et al., 1973) (Fig. 2–32K, L) with polytene chromosomes (Ivanovskaya, 1973).

2–3.4 Pollination and Double Fertilization

Florets at anthesis are forced open by the swelling of the lodicules. This may result from sugar influx with resulting osmotic swelling (Craig and O'Brien, 1975). Stamen filaments elongate with amazing rapidity, reaching three times their original length in about 3 min (Vries, 1971), which quickly exerts and exposes the anthers (Fig. 2–27, nos. 26–31).

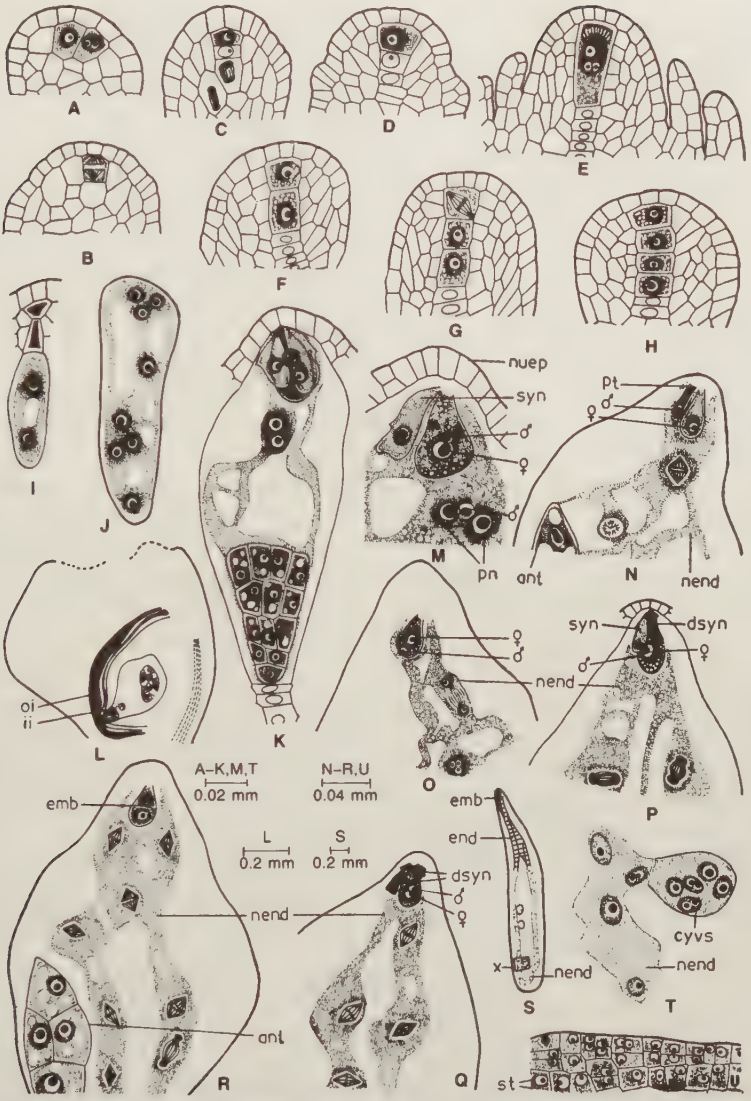

Fig. 2–32. Megasporogenesis, embryo sac development, fertilization, and endosperm development. *A*, ovule with two archesporial cells. *B–E*, Enlargement of megaspore mother cell; *F–H*, Meiosis and cytokinesis to form tetrad of megaspores; *I*, Three megaspores have degenerated and functional megaspore has undergone first mitosis; *J*, Two more mitoses have produced the 8-nucleate embryo sac; *K*, Mature embryo sac. Egg apparatus is at top, two central cell polar nuclei are intermediate, and a group of proliferated antipodal cells is at lower (chalazal) end; *L*, Mature embryo sac in relation to ovule and ovary (*oi*, outer integument; *ii*, inner integument); *M*, Fertilization. One synergid (*syn*) is intact and two sperms are in contact with egg and polar nuclei (*pn*), respectively; *N–P*, Stages of fertilization; *Q*, Early coenocytic endosperm nuclear divisions before zygote division; *R*, Two-celled proembryo surrounded by coenocytic endosperm antipodals (*ant*) still present; *S*, Endosperm is cellular (*end*) around embryo, coenocytic farther away (*nend*); *T*, Enlargement of area marked *x* in *S*, to show nuclear endosperm (*nend*) with multinucleate cytoplasmic vesicle (*cyvs*); *U*, Portion of cellular endosperm enlarged. From Deshpande and Raju (1979), with permission.

Stigmas are receptive for 4 to 13 days but pollen is viable for only 15 to 20 min, or up to 30 min under the best conditions (Vries, 1971). This short period of pollen viability is typical of grasses and other plant groups in which pollen is shed in the three-celled condition.

Wheat normally is self-pollinated. Pollen grains after their release from the anthers quickly become extremely dessicated. Because the stigma branches are not sticky, pollen is probably attracted by an initial brief electrostatic force followed quickly by absorption of water by the pollen grain through microscopic gaps in the stigma cuticle (Heslop-Harrison, 1979). Pollen may germinate within 1 min (Chandra and Bhatnagar, 1974). Only one grain usually germinates per stigma branch; if additional grains germinate, they soon swell and burst, and only one tube continues to grow (Rudramuniyappa and Panchaksharappa, 1974). A pollen tube penetrates a stigma papilla, grows through this cell, and then enters the central column of transmitting tissue in the style, where it grows between cells (Lange and Wojciechowska, 1976) until it enters similar transmitting tissue in the ovary wall. Investigators have not explained how the tube grows out of the ovary wall and enters the locule, but they agree that in 30 to 60 min after germination it enters the embryo sac (Bennett et al., 1973; Lange and Wojciechowska, 1976; Meyer, 1971).

A pollen tube enters the embryo sac by growing into the filiform apparatus of one synergid (Batygina, 1978; Deshpande and Raju, 1979). The filiform apparatus is a specialized area of the synergid wall, consisting of swollen wall material permeated with cytoplasmic channels appressed to the embryo sac wall. The pollen tube tip pushes through the filiform apparatus, then bursts and expels the sperm cells into the synergid. In some as yet unexplained manner, one sperm cell nucleus then enters the egg cell and fuses with its nucleus, thereby producing the zygote, the first cell of the embryo. The other sperm cell migrates to, and its nucleus fuses with, the polar nuclei to initiate the endosperm (Fig. 2–32M–Q).

2–3.5 Embryo and Endosperm Development

2–3.5.1 Coenocytic Endosperm and Proembryo

Fusion of polar nuclei of the central cell and one sperm nucleus produces the triploid primary endosperm nucleus. It first divides 5 to 6 h after fertilization (Bennett et al., 1973; Meyer, 1971; Morrison, 1955) and again about 6 h later. By the time the zygote divides, about 12 h (Meyer, 1971) or 24 h (Bennett et al., 1973; Morrison, 1955) after fertilization, or later in the 2nd day (Wojciechowska and Lange, 1977), there are already 16 to 32 endosperm nuclei (Fig. 2–32R). The endosperm therefore starts developing before the embryo, as is the rule among flowering plants.

Reports vary as to duration of the coenocytic (free-nuclear) endosperm stage. According to the most detailed study (Bennett et al., 1973), almost 10 cycles of nuclear division are initiated in nuclei near the mi-

cropyle, each cycle passing as a wave to the chalazal end. The nuclei lie in a common endosperm cytoplasm around the embryo sac periphery. A large vacuole is centrally located.

The intact synergid that did not receive the pollen tube has degenerated by the two- to four-celled proembryo stage (Fig. 2–32R). The clustered antipodal cells appear to synthesize protein, which they probably contribute to the rapidly growing coenocytic endosperm (Bennett et al., 1975). Antipodals eventually degenerate, and are rapidly resorbed, shortly after the endosperm becomes cellular (Bennett et al., 1973).

The early divisions in the zygote and subsequent embryo cells do not follow a precise sequence (Batygina, 1978; Bennett et al., 1973) but they always produce a club-shaped proembryo (Fig., 2–33A–F) (Batygina, 1978; Bennett et al., 1973; Deshpande and Raju, 1979). At the tip end, a few cells form the suspensor, an ephemeral structure that is inconspicuous and poorly defined in wheat and many other grasses (Batygina, 1978; Deshpande and Raju, 1979; Smart and O'Brien, 1983) (Fig. 2–33G). Although variable in size and shape among angiosperms, the suspensor is generally thought to be important for the nutrition and control of proembryo growth (Lersten, 1983). The term *proembryo* is not precisely defined, but it generally refers to embryo stages before the cotyledon, embryo axis, and radicle are evident.

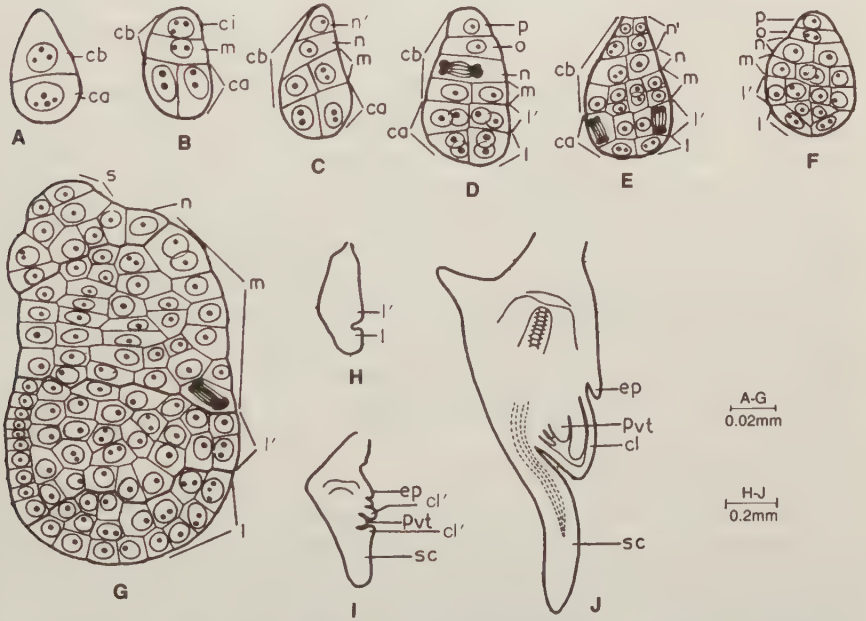

Fig. 2–33. Embryogeny. *A–F*, Stages in proembryo development. Suspensor is tip cell or two. Letters describe cell derivations; *G*, Proembryo just before organs become discernible; Suspensor (*s*) is inconspicuous; *H*, Apical notch delimits embryo axis and scutellum; *I*, Immature embryo with developing appendages. From Deshpande and Raju (1979), with permission.

2-3.5.2 Cellular Endosperm

Cell walls begin to form in the endosperm about 3 days post-pollination, after several hundred nuclei have formed and the proembryo has 8 to 10 cells (Bennett et al., 1973; Deshpande and Raju, 1979; Morrison, 1955). The first walls grow out from the embryo sac wall into the coenocytic endosperm. They are thought to be independent of association with spindle fibers (Mares et al., 1975; Mares et al., 1977; Morrison and O'Brien, 1976; Morrison et al., 1978), but a more recent study (Fineran et al., 1982) showed phragmoplasts and cell plates associated with even the earliest endosperm walls. Deshpande and Raju (1979) reported that endosperm first becomes cellular near the embryo (Fig. 2–32S), with peripheral cytoplasmic vesicles enclosing several nuclei (Fig. 2–32T). Cytoplasmic protrusions extend further into the central vacuole, and walls form within them. In this manner the entire embryo sac eventually becomes cellular and the vacuole disappears (Fig. 2–32U). After the first walls have formed, new walls form in the usual way, by means of a phragmoplast (Morrison and O'Brien, 1976).

The aleurone layer is partitioned off early by free wall formation (Morrison et al., 1978). Aleurone cells in the region of the crease become oblong or wedge-shaped, and have irregularly thickened and pitted walls. Once they have formed, these cells do not divide again, unlike the rest of the aleurone layer, which probably causes the crease to develop (Evers, 1970; Morrison et al., 1978) because adjacent endosperm continues to grow.

Starchy endosperm cells divide until 16 to 20 days after anthesis when about 100 000 cells have been produced (Briarty et al., 1979). These cells continue to enlarge until Day 35. Quantitative observations of changes in several endosperm characteristics during its 7-week period of development (Briarty et al., 1979) showed that starch is detectable by Day 6, and protein granules by Day 12. At the ultrastructural level, protein bodies are initiated as early as Day 6 (Bechtel et al., 1982) by Golgi vesicles that coalesce into small bodies and, by Day 30, into large bodies up to 100 μm in diameter (Pernollet and Camilleri, 1983). The membrane then ruptures and the protein bodies are transformed into matrix protein, which is diffuse and not in discrete bodies.

2-3.5.3 Proembryo to Mature Embryo

The proembryo begins to form the scutellum (Fig. 2–33G), and a notch develops to delimit it (Fig. 2–31H). The other embryo appendages then appear in rudimentary form (Fig. 2–33I). Further expansion and development leads to the mature embryo (Fig. 2–18).

During this period the embryo derives nutrients from surrounding tissues. The nucellar parenchyma and adjacent modified aleurone cells are hydrolyzed. Later, several layers of endosperm immediately surrounding the embryo appear devoid of reserves, and aleurone cells lying

Table 2–1. Characteristics of the different stages (I–V) in wheat caryopsis development.

	Stages				
	I	II	III	IV	V
Days post-anthesis†	0–7	7–14	14–21	21–31	31–50
Grain color	White	White/mint green	Green	Green	Tan
Grain length (mm)	<5.5	5.5–6.5	6.5–7.0	6.5–7.0	6.5
Grain fresh wt (mg)	<20	20–35	35–50	50–60	40–50
Endosperm characteristics	Watery	Milky, early dough	Soft-dough	Hard-dough	Hard
Pericarp characteristics	Fleshy	Shrinking	Reduced and flexible	Dry, thin and papery	Dry, thin, and papery
Embryo length‡ (mm)	<0.4	0.4–1.5	1.5–2.5	2.5–2.7	2.5–2.7

†Wheat cv. Chinese Spring grown in 18 h of light (19°C) and 6 h of dark (12°C).
‡Includes scutellum.

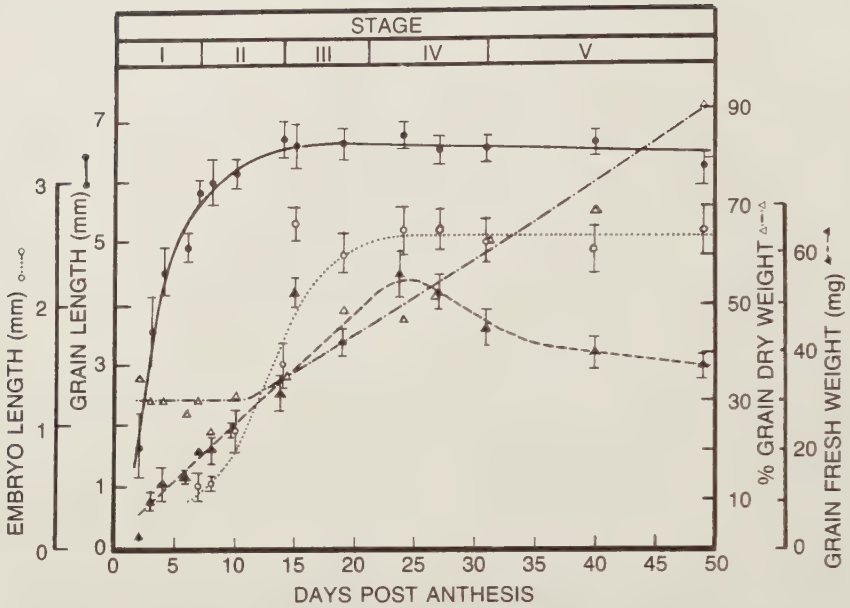

Fig. 2–34. Changes in four characteristics during 50 days of grain development. Each point represents the average of 12 to 45 grains or embryos, with bars representing one standard deviation. From Rogers and Quatrano (1983), with permission.

between the embryo and seed coat are hydrolyzed (Smart and O'Brien, 1983). The growing embryo therefore digests some endosperm, probably by secreting hydrolytic enzymes, before it becomes dormant in the mature grain.

2–3.5.4 Seedcoat and Caryopsis Coat Maturation

The integuments of the ovule are each only two cells thick (Fig. 2–16, no. 1). The outer integument begins to degenerate at about the time of zygote division, and it is obliterated before caryopsis maturity (Fig. 2–16, no. 2). The two innermost pericarp layers differentiate into cross- and tube-cell layers (Fig. 2–16, no. 3). The inner integument (Fig. 2–16, no. 3), which becomes the true seed coat, is just an acellular layer at maturity (Fig. 2–16, no. 4).

2–3.6 General Caryopsis Development

Table 2–1 and Fig. 2–34 summarize general changes during caryopsis development. Stages I to V are subdivisions of post-anthesis days. Most characteristics show progressive trends. Grains reach their full length by 15 days, and embryos reach final length by 25 days. After 10 days, dry weight increases steadily. Fresh weight, however, after a steady increase to about Day 24, declines slowly thereafter (Rogers and Quatrano, 1983).

The green color of the grain during Days 10 to 31 is because chloroplasts of cross cells show through the outer pericarp, which is translucent during this period (Percival, 1921). Later, the pericarp becomes dry, thin, and papery, and takes on the color of the mature grain.

REFERENCES

Aziz, P. 1972. Histogenesis of the carpel in *Triticum aestivum* L. Bot. Gaz. (Chicago) 133:376–386.

Bacic, A. and B.A. Stone. 1981. Isolation and ultrastructure of aleurone cell walls from wheat and barley. Aust. J. Plant Physiol. 8:453–474.

Batygina, T.B. 1971. Some peculiar features of macrosporogenesis and development of the female gametophyte in wheat. Ann. Univ. ARERS 9:46–50.

----. 1978. Embryology of wheat. Proc. Indian Natl. Sci. Acad. Part B 44:13–29.

Bechtel, D.B, R.L. Gaines, and Y. Pomeranz. 1982. Early stages in wheat endosperm formation and protein body initiation. Ann. Bot. 50:507–518.

Bennett, M.D., V. Chapman, and R. Riley. 1971. The duration of meiosis in pollen mother cells of wheat, rye and *Triticale*. Proc. R. Soc. London, B 178:259–275.

----., M.K. Rao, J.B. Smith, and M.W. Bayliss. 1973. Cell development in the anther, the ovule, and the young seed of *Triticum aestivum* L. var. Chinese Spring. Philos. Trans. R. Soc. London, B 266:39–81.

----., J.B. Smith, and I. Barclay. 1975. Early seed development in the Triticeae. Philos. Trans. R. Soc. London, B 272:199–227.

Bisalputra, T., W.J.S. Downton, and E.B. Tregunna. 1969. The distribution and ultrastructure of chloroplasts in leaves differing in photosynthetic carbon metabolism. I. Wheat, sorghum, and *Aristida* (Gramineae). Can. J. Bot. 46:15–21.

Blackman, E. 1969. Observations on the development of the silica cells of leaf sheath of wheat (*Triticum aestivum*). Can. J. Bot. 47:827–838.

----. 1971. The morphology and development of cross veins in the leaves of bread wheat (*Triticum aestivum* L.). Ann. Bot. 35:653–665.

Bradbury, D., M.M. MacMasters, and I.M. Cull. 1956a. Structure of the mature wheat kernel. II. Microscopic structure of pericarp, seed coat and other coverings of the endosperm and germ of hard red winter wheat. Cereal Chem. 33:342–360.

----, ----, and ----. 1956b. Structure of the mature wheat kernel. III. Microscopic structure of the endosperm of hard red winter wheat. Cereal Chem. 33:361–373.

----, ----, and ----. 1956c. Structure of the mature wheat kernel. IV. Microscopic structure of the germ of hard red winter wheat. Cereal Chem. 33:373–391.

Briarty, L.G., C.E. Hughes, and A.D. Evers. 1979. The developing endosperm of wheat (*Triticum aestivum* cultivar Kolibri): A stereological analysis. Ann. Bot. 44:641–658.

Bridges, I.G., and M.B. Wilkins. 1973. Growth initiation in the geotropic response of the wheat node. Planta 112:191–200.

Briggle, L.W. 1967. Morphology of the wheat plant. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:89–116.

----, and ----. 1963. Classification of *Triticum* species and of wheat varieties grown in the United States. USDA Tech. Bull. 1278. U.S. Government Printing Office, Washington, DC.

Brown, W.V. 1960. The morphology of the grass embryo. Phytomorphology 10:215–223.

----. 1965. The grass embryo—a rebuttal. Phytomorphology 15:274–284.

Busby, C.H., and T.P. O'Brien. 1979. Aspects of vascular anatomy and differention of vascular tissues and transfer cells in vegetative nodes of wheat. Aust. J. Bot. 27:703–711.

Campbell, W.P., J.W. Lee, T.P. O'Brien, and M.G. Smart. 1981. Endosperm morphology and protein body formation in developing wheat grain. Aust. J. Plant Physiol. 8:5–20.

Carolin, R.C., S.W.L. Jacobs, and M. Vesk. 1973. The structure of the cells of the mesophyll and parenchymatous bundle sheath of the Gramineae. Bot. J. Linn. Soc. 66:259–275.

Chambers, T.C., and C.D. Hamilton. 1973. Scanning electron microscopy of transfer cells: a new method for preparation of plant tissues. J. Microsc. (Oxford) 99:65–68.

Chandra, S., and S.P. Bhatnagar. 1974. Reproductive biology of *Triticum*. II. Pollen germination, pollen tube growth, and its entry into the ovule. Phytomorphology 24:211–217.

Chonan, N., H. Kawahara, and T. Matsuda. 1984. Development of the lipid globules in grass leaves of Kranz and non-Kranz type anatomy. Jpn. J. Crop Sci. 53:79–86.

Christensen, J.E., and H.T. Horner, Jr. 1974. Pollen pore development and its spatial orientation during microsporogenesis in the grass *Sorghum bicolor*. Am. J. Bot. 61:604–623.

Chrysler, M.A. 1906. The nodes of grasses. Bot. Gaz. (Chicago) 41:1–16.

Clowes, F.A.L. 1961. Apical meristems. Blackwell's Scientific Publications. Oxford.

Craig, S., and T.P. O'Brien. 1975. The lodicules of wheat: Pre- and post-anthesis. Aust. J. Bot. 23:451–458.

Dayanandan, P., F.V. Hebard, V.D. Baldwin, and P.B. Kaufman. 1977. Structure of gravity-sensitive sheath and internodal pulvini in grass shoots. Am. J. Bot. 64:1189–1199.

Deshpande, P.K., and P.S.G. Raju. 1979. Development of caryopsis and localization of DNA and proteins in *Triticum* spp. Phytomorphology 29:100–111.

Eleftheriou, E.P. 1984. Sieve-element plastids of *Triticum* and *Aegilops* (Poaceae). Plant Syst. Evol. 145:119–133.

Esau, K. 1965. Plant anatomy. 2nd ed. John Wiley and Sons, New York.

Evers, A.D. 1970. Development of the endosperm of wheat. Ann. Bot. 34:547–555.

Evert, R.F. 1980. Vascular anatomy of angiospermous leaves, with special consideration of the maize leaf. Ber. Dtsch. Bot. Ges. 93:43–55.

Fahn, A. 1982. Plant anatomy, 3rd ed. Pergamon Press, Elmsford, NY.

Fineran, B.A., D.J.C. Wild, and M. Ingerfeld. 1982. Initial wall formation in the endosperm of wheat, *Triticum aestivum*: A reevaluation. Can. J. Bot. 60:1776–1795.

Fulcher, R.G., T.P. O'Brien, and J.W. Lee. 1972a. Studies on the aleurone layer. I. Conventional and fluorescence microspcopy of the cell wall with emphasis on phenol-carbohydrate complexes in wheat. Aust. J. Biol. Sci. 25:23–34.

----, ----, and D.H. Simmonds. 1972b. Localization of arginine-rich proteins in mature seeds of some members of the Gramineae. Aust. J. Biol. Sci. 25:487–497.

Hayward, H.E. 1938. The structure of economic plants. The Macmillan Co., New York.

Hejnowicz, Z. 1959. Growth and cell division in the apical merstem of wheat roots. Physiol. Plant. 12:124–138.

Heslop-Harrison, J. 1979. An interpretation of the hydrodynamics of pollen. Am. J. Bot. 66:737–743.

Hitch, F.A., and B.C. Sharman. 1971. The vascular pattern of festucoid grass axes, with particular reference to nodal plexi. Bot. Gaz. (Chicago) 132:38–56.

Hu, S., C. Zhu, L. Xu, X. Li, and J. Shen. 1979. Ultrastructure of male gametophyte in wheat. I. The formation of generative and vegetative cells. (Chinese with English summary.) Acta Bot. Sin. 21:208–214.

Ivanovskaya, H.V. 1973. Functional morphology of polytene chromosomes of wheat antipodal cells. (Russian with English summary.) Tsitologiya 15:1445–1452.

Kuo, J., and T.P. O'Brien. 1974. Lignified sieve elements in the wheat leaf. Planta 117:349–353.

----, ----, and M.J. Canny. 1974. Pit-field distribution, plasmodesmatal frequency, and assimilate flux in the mestome sheath cells of wheat leaves. Planta 121:97–118.

----, ----, and S-Y Zee. 1972. The transverse veins of the wheat leaf. Aust. J. Biol. Sci. 25:721–737.

Lange, W., and B. Wojciechowska. 1976. The crossing of common wheat (*Triticum aestivum* L.) with cultivated rye (*Secale cereale* L.). I. Crossability, pollen grain germination and pollen tube growth. Euphytica 25:609–620.

Lee, D.R., and P.T. Atkey. 1984. Water loss from the developing caryopsis of wheat (*Triticum aestivum*). Can. J. Bot. 62:1314–1326.

Lersten, N.R. 1983. Suspensors in Leguminosae. Bot. Rev. 49:233–257.

Mares, D.J., K. Norstog, and B.A. Stone. 1975. Early stages in the development of wheat endosperm. I. The change from free nuclear to cellular endosperm. Aust. J. Bot. 23:311–326.

----, B.A. Stone, C. Jeffrey, and K. Norstog. 1977. Early stages in the development of wheat endosperm. II. Ultrastructural observations on cell wall formation. Aust. J. Bot. 25:599–614.

McQuade, H.A., and D.G. Pickles. 1980. Observations on synaptonemal complexes in premeiotic interphase of wheat. Am. J. Bot. 67:1361–1373.

Meyer, H. 1971. Blütenbiologische Untersuchungen bei Getreidekreuzungen. I. Das Wachstum von Roggen- und Weizenpollen-schläuchen in den Weizennarbe und die Entwicklung des Fruchtknotens bis 48 Stunden nach der Bestäubung. Arch. Zuechtungsforsch. 1:171–183.

Miki, N.K., K.J. Clarke, and M.E. McCully, 1980. A histological and histochemical comparison of the mucilages on the root tips of several grasses. Can J. Bot. 58:2581–2593.

Morrison, I.N., J. Kuo, and T.P. O'Brien. 1975. Histochemistry and fine structure of developing wheat aleurone cells. Planta 123:105–116.

----, and T.P. O'Brien. 1976. Cytokinesis in the developing wheat grain; division with and without a phragmoplast. Planta 130:57–67.

----, ----, and J. Kuo. 1978. Initial cellularization and differentiation of the aleurone cells in the ventral region of the developing wheat grain. Planta 140:19–30.

Morrison, J.W. 1955. Fertilization and post-fertilization development in wheat. Can. J. Bot. 33:168–176.

Murphy, G.J.P., and M.L. Parker. 1984. Lipid composition and carbon turnover of wheat leaf oleosomes. J. Exp. Bot. 35:348–355.

Negbi, 1984. The structure and function of the scutellum of the Gramineae. Bot. J. Linn. Soc. 88:205–222.

O'Brien, T.P., and J. Kuo. 1975. Development of the suberized lamella in the mestome sheath of wheat leaves. Aust. J. Bot. 23:783–794.

----, and K.V. Thimann. 1965. Histological studies on the coleoptile. I. Tissue and cell types in the coleoptile tip. Am. J. Bot. 52:910–918.

----, and S-Y. Zee. 1971. Vascular transfer cells in the vegetative nodes of wheat. Aust. J. Biol. Sci. 24:207–217.

----, ----, and J.G. Swift. 1970. The occurrence of transfer cells in the vascular tissues of the coleoptilar node of wheat. Aust. J. Biol. Sci. 23:709–712.

Opatrna, J., F. Seidlova, and K. Benes. 1964. The anatomy of the shoot apex of wheat (*Triticum aestivum* L.) during transition from the vegetative to the reproductive state and the determination of the primordia. Biol. Plant. 6:219–225.

Pal, B.P., S. Ramanujam, and A.R. Memon. 1952. Evaluation of vegetative characters as classificatory aids in classifying crop plants. I. Leaf-hairiness in *Triticum*. Indian J. Genet. Plant Breed. 12:15–24.

Parker, M.L., and G.J.P. Murphy. 1981. Oleosomes in flag leaves of wheat: Their distribution, composition and fate during senescence and rust-infection. Planta 152:36–43.

Patrick, J.W. 1972a. Vascular system of the wheat plant. I. Mature state. Aust. J. Bot. 20:49–63.

----. 1972b. Vascular system of the stem of the wheat plant. II. Development. Aust. J. Bot. 20:65–78.

Percival, J. 1921. The wheat plant. A monograph. E.P. Dutton and Co., New York.

Pernollet, J.C., and C. Camilleri. 1983. Formation and development of protein bodies in the wheat endosperm. Physiol. Veg. 21:1093–1103.

Pickett-Heaps, J.D., and D.H. Northcote. 1966. Cell division in the formation of the stomatal complex of the young leaves of wheat. J. Cell Sci. 1:121–128.

Prankerd, T.L. 1920. Statocytes of the wheat haulm. Bot. Gaz. (Chicago) 70:148–152.

Rogers, S.O., and R.S. Quatrano. 1983. Morphological staging of wheat caryopsis development. Am. J. Bot. 70:308–311.

Rudramuniyappa, C.K., and M.G. Panchaksharappa. 1974. Histochemistry of pollen tube growth *in vivo* in *Triticum durum* Desf. Cytologia 39:665–671.

Sasahara, T. 1982. Influence of genome on leaf anatomy of *Triticum* and *Aegilops*. Ann. Bot. 50:491–497.

Sharman, B.C. 1983. Developmental anatomy of the inflorescence of bread wheat (*Triticum aestivum* L.) during normal initiation and when affected by 2.4-D. Ann. Bot. 52:621–639.

----, and P.A. Hitch. 1967. Initiation of procambial strands in leaf primordia of bread wheat, *Triticum aestivum* L. Ann. Bot. 31:229–242.

Smart, M.G., and T.P. O'Brien. 1979a. Observations on the scutellum. I. Overall development during germination in four grasses. Aust. J. Bot. 27:391–401.

----, and ----. 1979b. Observations on the scutellum. II. Histochemistry and autofluorescence of the cell wall in mature grain and during germination of wheat, barley, oats and rye grass. Aust. J. Bot. 27:403–411.

----, and ----. 1983. The development of the wheat embryo in relation to the neighboring tissues. Protoplasma 114:1–13.

Swift, J.G., and T.P. O'Brien. 1970. Vascularization of the scutellum of wheat. Aust. J. Bot. 18:45–53.

----, and ----. 1971. Vascular differentiation in the wheat embryo. Aust. J. Bot. 19:63–71.

----, and ----. 1972a. The fine structure of the wheat scutellum before germination. Aust. J. Biol. Sci. 25:9–22.

----, and ----. 1972b. The fine structure of the wheat scutellum during germination. Aust. J. Biol. Sci. 25:469–486.

Teare, I.D., C.J. Peterson, and A.G. Law. 1971. Size and frequency of leaf stomata in cultivars of *Triticum aestivum* and other *Triticum* species. Crop Sci. 11:496–498.

Thimann, K.V., and T.P. O'Brien. 1965. Histological studies on the coleoptile. II. Comparative vascular anatomy of coleoptiles of *Avena* and *Triticum*. Am. J. Bot. 52:918–923.

Troughton, J., and L.A. Donaldson. 1972. Probing plant structure. McGraw-Hill Book Co., New York.

----, and F.B. Sampson. 1973. Plants, a scanning electron microscope survey. John Wiley and Sons, New York.

Vries, A.P. de. 1971. Flowering biology of wheat, particularly in view of hybrid seed production—a review. Euphytica 20:152–170.

Waller, S.S., and J.K. Lewis. 1979. Occurrence of C_3 and C_4 photosynthetic pathways in North American grasses. J. Range Manage. 32:12–28.

Wettstein-Knowles, P. von. 1974. Ultrastructure and origin of epicuticular wax tubes. J. Ultrastruct. Res. 46:483–498.

Williams, R.F. 1975. The shoot apex and leaf growth. Cambridge University Press, Cambridge.

----, B.C. Sharman, and R.H.M. Langer. 1975. Growth and development of the wheat tiller. I. Growth and form of the tiller bud. Aust. J. Bot. 23:715–743.

Wojciechowska, B., and W. Lange. 1977. The crossing of common wheat (*Triticum aestivum* L.) with cultivated rye (*Secale cereale* L.). II. Fertilization and early post-fertilization developments. Euphytica 26:287–297.

Zee, S.-Y., and T.P. O'Brien. 1970. Studies on the ontogeny of the pigment strand in the caryopsis of wheat. Aust. J. Biol. Sci. 23:1153–1171.

----, and ----. 1971a. Vascular transfer cells in the wheat spikelet. Aust. J. Biol. Sci. 24:35–49.

----, and ----. 1971b. The vascular tissue of the lodicules of wheat. Aust. J. Biol. Sci. 24:805–809.

3 Growth, Development, and Physiology

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This chapter presents an overview of topics associated with growth and development of wheat (*Triticum aestivum* L.), with particular attention to those events and physiological processes that directly influence grain yield and quality. It can serve as an access to more extensive consideration of each topic. Several other general reviews of wheat physiology exist (Austin and Jones, 1975; Evans et al., 1975; Evans and Wardlaw, 1976; Langer and Dougherty, 1976).

3–1 PHYSIOLOGICAL HISTORY

Diploid and tetraploid wheat were first domesticated in the Middle East at least 9000 yr ago. In agriculture, seed saved from a previous crop generation is deliberately sown to produce the following crop. This differs greatly from the situation where wild stands are gathered and each new generation is produced from nonharvested seed dispersed by natural processes. Domestication had a great effect on wheat, with results such as reduced grain shattering and increased inflorescence size (Harlan, 1975). More than 6000 yr ago, hybridization of a tetraploid and diploid to produce hexaploid bread wheat broadened the range of adaptation of domesticated wheat (Zohary et al., 1969).

The domestication of wheat and the subsequent increase in ploidy caused shifts in morphological and physiological characteristics. Modern tetraploid and hexaploid wheat genotypes have larger leaves and grain than wild forms of the diploid (Evans and Dunstone, 1970). Domestication has shortened the tillering phase, resulting in fewer spikebearing tillers per plant for modern wheat. The harvest index (proportion of aboveground plant mass in the grain) and grain growth rate are higher in modern wheat (Evans and Dunstone, 1970). The grain in modern wheat is more dependent on the leaves than the spike for photoassimilate,

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as well as on greater remobilization of assimilate from stems. Photosynthetic rate per unit of leaf area and crop growth rate, however, have not increased during domestication (Evans and Dunstone, 1970). Other comparisons of physiological characteristics in wild and domesticated wheat are available (Singh and Tsunoda, 1978; Kishitani and Tsunoda, 1981).

Researchers have recently become interested in documenting changes that have occurred in wheat during this century when scientific plant breeding techniques have been extensively used. Austin et al. (1980) found that newer, higher-yielding winter wheat cultivars in the United Kingdom were shorter and earlier maturing, and often bore more spikes than older cultivars. Increased grain yield with modern cultivars was largely attributed to greater distribution of aboveground dry mass to the grain. Similarly, Jensen (1978a) noted a decline in crop height associated with the substantial yield improvement in New York winter wheat during this century.

What physiological modifications will assist in achieving future yield enhancements in wheat? Some researchers (Jensen, 1978a; Evans, 1980) believe that extending historic rates of yield increase into the future will be hindered by biological and economic constraints. Further increases in harvest index may be possible, but genetic gain in yield potential will ultimately depend on increasing total crop growth and biological yield. Austin (1982) queried the physiological basis for achieving higher biological yield. He concluded that net crop photosynthetic capacity might be enhanced by increasing leaf area index at anthesis, delaying leaf senescence, and decreasing respiratory loss of assimilates. Some modifications, such as delaying senescence, may be attractive in environments where soil moisture is not limiting. In moisture-limited environments, the approach of choice may be to increase productivity under stress or to improve the inherent efficiency of the photosynthetic process in a way that does not require additional water.

3–2 VEGETATIVE DEVELOPMENT

3–2.1 Germination and Seedling Emergence

The wheat embryo in an ungerminated kernel possesses three to six seminal root primordia, a number determined by cultivar and kernel size (Klepper et al., 1984). The embryo may also have initiated tiller bud primordia in the axils of the coleoptile and first true leaf during its development on the mother plant (Stern and Kirby, 1979; Peterson et al., 1982).

Minimum moisture for germination in wheat is 35 to 45% of kernel dry weight (Evans et al., 1975). Germination may occur at temperatures between 4 and 37°C with 12 to 25°C being considered optimum (Austin and Jones, 1975). Minimum, optimum, and maximum temperatures for germination vary with other environmental conditions, as well as with

genotype and seed age. For example, the minimum temperature for seedling emergence was found to be slightly lower when soil moisture availability was restricted, suggesting a compensation for adverse moisture conditions (DeJong and Best, 1979). However, researchers have noted that germination and emergence generally requires more time or accumulated heat units as soil water potential is reduced below field capacity (Lindstrom et al., 1976; DeJong and Best, 1979). The heat units required for emergence also increases with greater seeding depth.

During germination, the seminal roots extend first, followed by the coleoptile. Seminal roots at the level of the seed are associated with the scutellar and epiblast nodes. In addition to the seminal root system, adventitious roots are produced in association with the coleoptilar node. A distance usually develops between this complex of roots and those adventitious roots originating from the crown region, caused by elongation of the internode between the coleoptilar node and the first foliar node. The extent of elongation of this internode varies with planting depth. When the coleoptile emerges from the soil its growth ceases and the first true leaf pushes through its tip. Before the first leaf becomes functional photosynthetically, the seedling depends on energy and nutrients provided by the reserves in the kernel. Accordingly, within a genotype larger kernels or higher kernel N concentrations may produce more vigorous seedlings (Austenson and Walton, 1970; Lowe and Ries, 1972).

Semidwarf plant stature attributed to the genes Rht_1 or Rht_2 is generally associated with a shorter coleoptile and reduced seedling vigor (Allan et al., 1962; Allan, 1980), although the particular manifestations of semidwarf stature depend on the genetic background into which these genes are introduced. Shallower sowing depths and higher seeding rates have been used to overcome problems of stand establishment associated with semidwarf cultivars.

3–2.2 Leaf Development

The embryo in the kernel contains up to three leaf primordia (Austin and Jones, 1975). After germination, the vegetative shoot apex initiates additional leaf primordia. The number of leaf primordia varies from 7 to 15 (Kirby, 1983), the final number being influenced by genotype, temperature, light intensity, and nutritional status of the plant. The rate of leaf initiation is about 0.35 primordia per day for spring wheat grown under controlled environment conditions of 17/12°C (day:night temperature) and 16-h daylength (Fig. 3–1). Rate of primordium initiation increases with higher temperature and light intensity (Friend et al., 1962). Delayed sowing of spring wheat causes a shortened duration of leaf initiation, but an increased rate (Stern and Kirby, 1979).

The rate of leaf primordium initiation is greater than the rate of leaf appearance. Accordingly, two or three leaf primordia in addition to those present in the dry seed may already be initiated by the time the first leaf emerges from the coleoptile. Thus, the rate of leaf area development, an

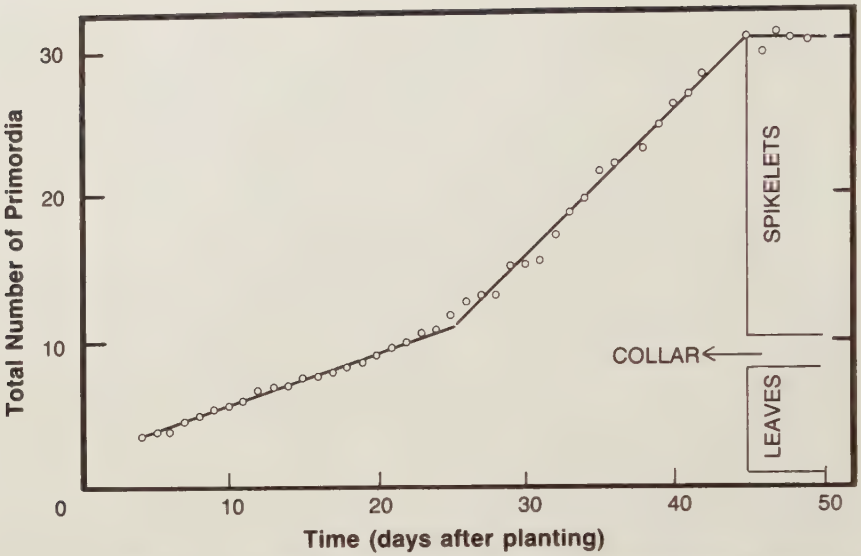

Fig. 3–1. Total number of leaf and spikelet primordia at various times after planting in spring wheat (Kirby, 1974).

important production consideration, is influenced more by the rate of leaf appearance than by the rate of leaf initiation.

The rate of leaf appearance is influenced by temperature. Bauer et al. (1984) have proposed that standard maturity cultivars of spring wheat in the north-central USA require about 80 growing degree units (Celsius scale) per leaf. Early cultivars may require slightly fewer degree units to develop each leaf. Kemp and Blacklow (1982) showed a curvilinear relationship between leaf extension rate and temperature. The minimum temperature for leaf extension was approximately O °C, the optimum 28 °C, and the maximum greater than 38 °C. Differences in leaf appearance rate have been observed among cultivars and between the main shoot and tillers on the same plant (Kirby et al., 1983).

Mature leaf size varies with the leaf's position on the plant. The size of successive leaves usually increases. Leaf width and thickness may increase with higher light intensity or temperature, but leaf length accordingly decreases (Friend et al., 1962). Maximum leaf area per shoot is achieved about the time the flag leaf has fully expanded, which occurs just before heading.

3–2.3 Root Development

With very deep sowing, more than one node may develop below the soil surface, each bearing roots (Hadjichristodoulou et al., 1977). Root axes are produced at predictable times in relation to shoot development, and the total number of roots formed is associated with the number of leaves on a culm and the degree of tillering (Klepper et al., 1984). Crown

roots originating from the main shoot begin to appear at about the time that tillers first emerge (Fig. 3–2). Roots originating from tillers generally develop after a tiller has formed three leaves (Fig. 3–2).

Whether plant stature influences rooting pattern and depth is of concern since semidwarf cultivars have become so important in world wheat production. MacKey (1973) concluded that root growth of a genotype was proportional to its top growth. However, Lupton et al. (1974) maintained that semidwarf cultivars of winter wheat had more extensive root systems than taller cultivars. Cholick et al. (1977), evaluating tall and semidwarf winter wheat genotypes under semiarid conditions, concluded that no relationship exists between cultivar height and rooting depth. Questions obviously remain, but the successful development of semidwarf cultivars for semiarid areas indicates that these cultivars can extend their roots to adequate depths to supply moisture throughout development under dry conditions.

3–2.4 Tillering

Tiller production can be important in determining grain yield (Simons and Hunt, 1983). A typical time course for shoot production in winter wheat under European conditions is shown in Fig. 3–3 (Darwinkle, 1978). Similar trends have been observed for winter wheat in North America (Simons, 1982) and for spring wheat (Power and Alessi, 1978).

Tiller appearance is closely associated with leaf emergence (Masle-

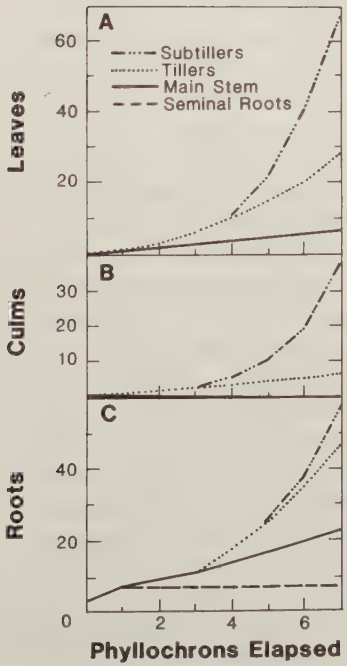

Fig. 3–2. Cumulative numbers of leaves, culms, and roots on a winter wheat plant, as related to elapsed phyllochrons (Klepper et al., 1984).

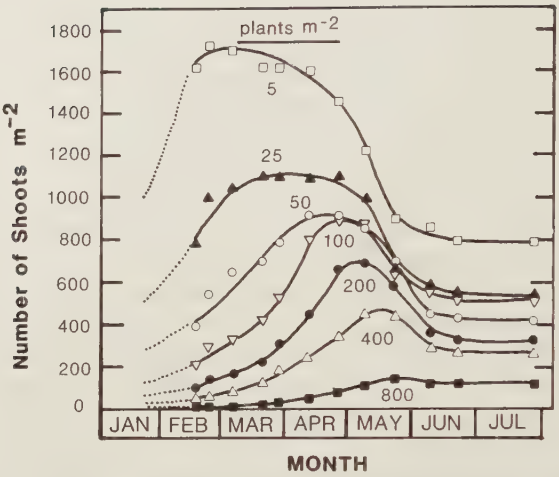

Fig. 3–3. Shoot number trends over the growing season for winter wheat sown at different plant densities (Darwinkle, 1978).

Meynard and Sebillotte, 1981; Kirby et al., 1983) and follows a well-defined, ordered pattern. The tillers formed in the axils of the coleoptile and the first true leaf usually emerge first. In general, three phyllochrons separate the emergence of a leaf and its subtended tiller (one phyllochron is the interval between two successive leaves) (Kirby et al., 1983). Rickman et al. (1983) described the ordered sequence of primary tiller formation in relation to degree unit accumulation. They noted that stress conditions such as dry or crusting soil might hinder the formation of some tillers, but that once the stress is removed, subsequent tillers form normally.

The coleoptilar tiller forms sporadically, and its appearance depends on genotype, planting rate and depth, irradiance, temperature, and seed size (Rawson, 1971b; Peterson et al., 1982). Excision of the endosperm before germination or removal of the first foliage leaf blade after emergence both reduce the frequency of coleoptilar tiller appearance.

Primary tiller buds can form in the axils of the first four or more true leaves of the main shoot. In addition, subtillers can develop from primary or secondary tillers, particularly in spaced plants (Fig. 3–2).

The newly formed tiller primordium first enlarges and establishes a protective prophyll. The bud then elongates and produces leaf primordia. Fewer total leaves are produced by tillers, compared to the main shoot, which serves to help synchronize the onset of spike initiation among shoots on the plant (Fig. 3–4). When a tiller bud reaches a length of 0.7 to 5 mm its relative growth rate declines, but then increases again if it emerges (Williams and Langer, 1975).

In winter wheat, a few tillers may form in the autumn or winter if conditions are mild. With warmer spring temperatures, there is a rapid increase in tiller number (Fig. 3–3). For winter or spring wheat, the main

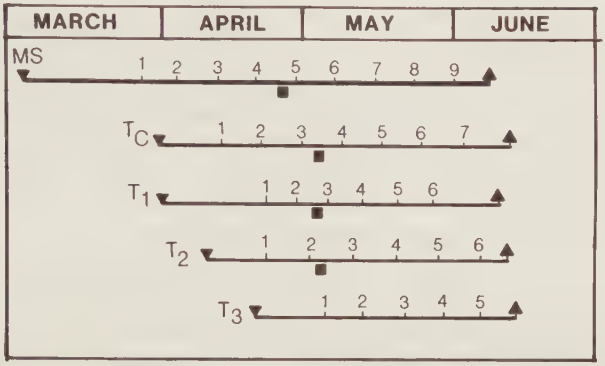

Fig. 3–4. The developmental pattern of the main shoot (MS), the coleoptile tiller (T_c), and tillers 1, 2 and 3 (T_1, T_2, T_3) for 'Kolibri' spring wheat. Numbers above the lines are the numbers of expanded leaves. The symbols represent: ▼, sowing time; ■, observation of double ridges; ▲, spike emergence. (Adapted from Stern and Kirby, 1979.)

shoot and earlier-formed tillers (those formed when leaves 4 to 6 emerge on the main shoot) are most likely to complete development and form grain (Kirby, 1983). Later formed tillers usually senesce prematurely in a crop community environment. Masle-Meynard (1981) found that only tillers that develop past the three-leaf stage and form roots survive to form a spike under conditions where soil nitrogen is limiting.

The proportion of tillers that senesce prematurely varies with cultivar (Simons, 1982), N nutrition (Power and Alessi, 1978), temperature (Ishag and Taha, 1974), and plant population (Darwinkle, 1978; Fig. 3–3). Cessation of tillering and onset of tiller senescence are commonly associated with the completion of spikelet initiation on the main shoot and the beginning of stem elongation (Kirby and Appleyard, 1981; Simons, 1982).

Controversy exists regarding the value of tillers that abort without bearing grain. There seems little doubt that senescing tillers remobilize nitrogenous and other organic substances to surviving shoots (Lupton and Pinthus, 1969; Rawson and Donald, 1969). Furthermore, tillers destined to senesce may translocate a portion of their current photoassimilate directly to surviving shoots even before visible signs of senescence are apparent. Despite their potential resource contributions, unproductive tillers may be undesirable (Rawson and Donald, 1969). Innes et al. (1981) noted that water consumption by unproductive tillers has particularly adverse consequences in dry areas. These researchers found that genotypes selected for high spike numbers (also possessing higher tiller mortality) gave 8% less yield than low-tillering, high-survival lines in an environment where pre-anthesis drought occurred. Such conditions usually cause higher tiller mortality. Water consumed by sterile tillers in such circumstances likely reduces the productive capacity of surviving shoots. Reducing tiller mortality might be achieved through plant breeding or N management.

Recently, interest has been expressed in modifying tillering habit of

wheat by exogenous applications of growth regulators. Kettlewell et al. (1983) applied 2-chloroethyltrimethyl ammonium chloride (chlormequat chloride, CCC) to winter wheat when plants had three leaves. They concluded that such early applications of chlormequat increased tiller survival and possibly also increased tiller production. Yield was not affected significantly by the chlormequat treatment.

3–2.5 Stem Development

Stem elongation begins when most florets on the developing spike have initiated stamen primordia, which corresponds closely to the formation of the terminal spikelet (Kirby and Appleyard, 1981). Stem elongation coincides with the growth of leaves, tillers, roots, and the inflorescence, which raises questions about possible competition for limited assimilate supplies (Patrick, 1972).

Lower internodes of the stem remain short, with the fourth internode elongating first in a spring wheat plant possessing nine total leaves (Kirby and Appleyard, 1981). In winter wheat, which usually forms more leaves, a higher numbered internode is first to elongate. When an internode has elongated to about half its final length, the internode above it begins elongating. This sequence continues until stem elongation is complete, usually near anthesis. Each succeeding stem internode is progressively longer; the final stem segment to elongate, the peduncle, can account for as much as half of the total stem length (Evans et al., 1975).

The height of wheat ranges from about 30 to 150 cm and is influenced by both the genotype and the growing conditions. Genotypes possessing both the Rht_1 and Rht_2 dwarfing genes are shorter than those with only one dwarfing gene, which in turn are shorter than those with neither gene (Allan, 1983). As a rule, variation in height is due more to differences in internode length than internode number (Austin and Jones, 1975). Exogenously applied growth regulators that reduce stem internode elongation and stem length are now used commercially to suppress lodging.

3–3 REPRODUCTIVE DEVELOPMENT

3–3.1 Pre-anthesis Spike Development and Grain Set

The double-ridge stage on the shoot apex has traditionally been regarded as the beginning of spike development. However, Kirby (1974) showed that double ridges were not visible until about half the spikelet primordia had already been initiated. Stern and Kirby (1979) accordingly proposed that the shift to reproductive development more closely corresponds to elongation of the apical dome, which occurs in spring wheat when the main shoot has about three full leaves. Spikelet initiation occurs earlier for tillers; for example, the tiller formed in the axil of the first true

leaf on the main shoot of spring wheat begins initiating spikelets when it has only one to two leaves (Stern and Kirby, 1979).

The rate of spikelet initiation is about two to three times greater than that for the leaf primordia (Fig. 3–1). Spikelet initiation rate on tillers equals or exceeds that on the main shoot (Stern and Kirby, 1979), which helps to synchronize more closely the time of terminal spikelet formation and spike emergence among shoots on a plant (Fig. 3–4). Delayed planting increases the rate of spikelet initiation. Cultivar differences also exist (Stern and Kirby, 1979).

Photoperiod is important in determining the number of spikelets initiated. Longer photoperiod induces earlier spike initiation and increases spikelet initiation rate. However, earlier terminal spikelet formation causes fewer total spikelets to be formed (Rawson, 1971a; Allison and Daynard, 1976). Temperature interacts in establishing response to photoperiod, but its influence is less when photoperiod is long (Austin and Jones, 1975). When day/night temperature was increased from 16/9°C to 23/16°C under controlled environment conditions, the rate of spikelet initiation increased, but its duration was shorter. With an additional increase to 30/23°C both rate and duration of spikelet initiation declined causing fewer spikelets to be formed (Rahman and Wilson, 1978).

In winter wheat, floral development is promoted by exposure of seedlings to low temperatures (vernalization), with 3 to 8°C considered most effective. Genotypes differ in their response to vernalizing temperatures (Austin and Jones, 1975).

Near the end of spikelet initiation, floret differentiation within spikelets begins in the lower-central portion of the spike and proceeds both upward and downward. This establishes a development hierarchy within the spike that persists through anthesis and grain growth. Initiation of the terminal spikelet marks the end of spikelet formation (Kirby and Appleyard, 1981). A spikelet can initiate up to 12 floret primordia; however, the distally positioned florets in a spikelet fail to develop and usually only five or fewer florets bear kernels. Conditions that influence spikelet number, such as temperature, daylength, and genotype, also influence the number of florets formed per spikelet. Kirby (1974) found no differences in the rate of floret differentiation among spikelets within the spike, but since floret differentiation begins later in basal or terminal spikelets these form fewer total florets. Stockman et al. (1983) showed that light enhancement or shading during an 8-day period of floret development substantialy altered the number of competent florets at anthesis and the number of kernels formed per spikelet. The treatment effects were greater in the basal or distal spikelets of the spike than in the central ones. Increases in kernel number prompted by assimilate enhancement were attributed to greater floret survival. Sucrose supply to a developing spikelet appears to be important for its development and may be potentially limiting, especially at high seeding rates (Scott et al., 1975; Mohaptra et al., 1982).

Throughout the pre-anthesis period, differences in duration of the various developmental phases among shoots on the same plant, among spikelets within the same spike, and among florets within the same spikelet all serve to synchronize development. For example, a difference of several weeks in the initiation of various shoots on a plant is reduced to only a few days by the time of spike emergence (Fig. 3–4). Similarly, the difference in time of initiation between the first two florets in a spikelet may be more than 2 days, but the time differential between these florets at meiosis may be only 6 h (Kirby, 1974). Meiosis occurs when the developing anthers are green and about 1-mm long, and at about the same time in both the anthers and carpel (Kirby and Appleyard, 1981).

Wheat florets have two lodicules located at the base of the ovary that swell during anthesis and function to open the flower for anther extrusion (Craig and O'Brien, 1975). Within 20 min after the lodicules swell the lemma and palea close and anthesis is complete. The increase in osmotic pressure causing swelling of the lodicules likely results from a rapid sugar influx. The lodicules are extensively vascularized with phloem transfer cells (Craig and O'Brien, 1975). It is clear that the swelling of the lodicules, the extension of the staminal filaments, and the unfurling of the stigma arms during anthesis are all highly coordinated events and may be controlled by the same process (Craig and O'Brien, 1975). An aberration of this sequence occurs in florets of some male-sterile wheat genotypes where florets may remain open for several days. This suggests that the collapse of the lodicules which causes floret closure may be linked to pollination or fertilization (Craig and O'Brien, 1975).

There is an interaction among florets at anthesis that influences the number of kernels ultimately formed. Sterilization of proximal florets within central spikelets 2 days before anthesis causes compensatory grain set in distal florets (within the same spikelets) that normally are not fertile. There also may be additional grain set in the basal and top portions of the spike (Rawson and Evans, 1970). Presence of viable ovaries in proximal spikelets prevents distal florets from setting grain (Evans et al., 1972). Grain set in distal florets is possible when the proximal florets lose their viability. These observations suggest a correlative, hormonal regulation of grain set. Radley (1980) showed that abscisic acid or gibberellic acid exogenously applied to spikes prevented grain set in some or all of the florets in a spikelet.

Differences in spike development and grain set between semidwarfs and tall genotypes are of considerable interest. Conceivably, semidwarf have more assimilate available for spike development, since their assimilate investment in stem growth may be lower. This could result in higher floret survival and more kernels formed per spikelet or spike. In a comparison of a semidwarf and a tall cultivar, Bremner and Davidson (1978) concluded that higher kernel numbers in their semidwarf were attributable to lower floret mortality. Brooking and Kirby (1981) also found more potentially fertile florets in semidwarf lines, particularly in the basal por-

tion of the spike. They emphasized the importance of assimilate supply during the floret development period and proposed that presence of a dwarfing gene enhanced partitioning of assimilate to the spike.

3–3.2 Kernel Development

Growth of kernels progresses in several phases (Fig. 3–5). Dry weight accumulation is slow just after anthesis, during which time endosperm cell division occurs and cell numbers increase rapidly (Wardlaw, 1970). The number of endosperm cells formed by a kernel ultimately influences its rate of growth and final weight (Brocklehurst, 1977; Singh and Jenner, 1982). Rates of endosperm cell division or final cell numbers are influenced by light intensity, water stress, temperature, and genotype (Wardlaw, 1970; Wardlaw, 1971; Brocklehurst, 1977; Brocklehurst et al., 1978).

Starch deposition begins 1 to 2 weeks following anthesis and initiates a period of nearly linear increase in kernel dry weight (Fig. 3–5). The duration of this uniform growth period varies (depending on the temperature, water stress, and genotype), but usually lasts for 2 to 4 weeks (Spiertz and Ellen, 1978; Martinez-Carrasco and Thorne, 1979; Simmons

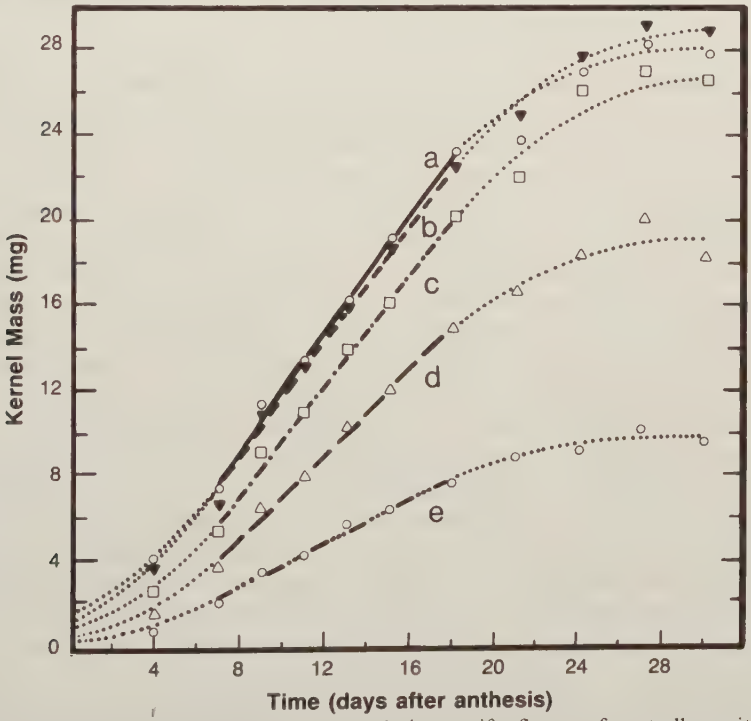

Fig. 3–5. Dry matter accumulation by kernels in specific florets of centrally-positioned spikelets for spring wheat genotype 8037. Kernels are sequentially designated by the letters *a* through *e*, starting with kernel closest to the spike rachis (Simmons and Crookston, 1979).

and Crookston, 1979). Since most of the final weight of the kernel is accumulated during this relatively brief period, it is not surprising that the rate of growth during this time is closely associated with the final weight achieved (Sofield et al., 1977a; Simmons and Crookston, 1979). Reductions in assimilate supplies to kernels may result in reduced growth, particularly if the reduction occurs early in development (Simmons et al., 1982). Similarly, enhanced assimilate availability during the linear growth period may also increase kernel growth rate (Simmons et al., 1982), although conditions during the early stages of grain filling, when growth potential is established, may restrict the kernel's capacity to accumulate starch later (Jenner, 1979). Temperature also substantially influences kernel growth rates, likely through its direct effect on kernel development rather than through secondary effects on availability of photosynthate (Wardlaw et al., 1980; Bhullar and Jenner, 1983).

The growth and final weight of an individual kernel depends on the spikelet and floret position at which it forms (Rawson and Evans, 1970; Bremner, 1972; Kirby, 1974; Simmons and Moss, 1978a). Kernels formed in the centrally positioned spikelets and in the proximal florets within an individual spikelet are usually largest (Fig. 3–5). This hierarchy for kernel weight within the spike is already evident at anthesis. Kirby (1974) found a significant correlation between final kernel weight and time of floret initiation, which indicates that the duration and sequence of ovary formation within the spike may be important in establishing grain weight. Final kernel weight is generally associated with the weight of the ovary at anthesis (Singh and Jenner, 1982), although exceptions exist, such as in the case of the first two proximal kernels within a spikelet. When assimilate supplies are adequate, the second kernel usually has a higher final weight than the first kernel, although its ovary is initially smaller at anthesis (Bremner and Rawson, 1978) (Fig. 3–5). The inherent capacity for growth of the first kernel may be limited such that it cannot fully benefit from its favorable position within a spikelet.

Absolute rates of kernel growth during the linear growth period in the field are often between 1.4 and 2.0 mg kernel^{-1} day^{-1}. They may vary considerably depending on growth conditions, genotype, and kernel position within the spike (Simmons and Crookston, 1979; Houseley et al., 1982; Simmons et al., 1982; Singh and Jenner, 1982; Simmons and Busch, 1984) (Fig. 3–5). Kernels formed in distally positioned florets within a spikelet have a lower growth rate than proximal kernels (Fig. 3–5). When kernel number per spike is artificially reduced early in grain filling, which provides additional assimilate to the distal kernels, they respond with an enhanced growth rate and achieve higher final weights (Simmons et al., 1982; Simmons and Busch, 1984). The growth rate potential for proximal kernels in centrally positioned spikelets may approach 2.5 to 3.0 mg kernel^{-1} day^{-1} (Simmons et al., 1982; Simmons and Busch, 1984).

Mineral accumulation by kernels follows a pattern similar to that for dry matter. The concentration of N or P in grains declines during the

first few days after anthesis, then rises slowly (Sofield et al., 1977b). Kernels formed in distal florets of individual spikelets usually have a lower N concentration than proximal kernels (Bremner, 1972; Simmons and Moss, 1978a). Artificial reductions in kernel number per spike result in elevated N concentrations in the remaining kernels (Simmons and Moss, 1978a; Radley and Thorne, 1981; Thorne 1981;), suggesting that control of N movement into kernels may be independent of carbohydrate movement. Such results imply that the cause of low N concentration in grain is inadequate supply of N to the kernels (Jenner, 1980; Thorne, 1981).

Nitrogen uptake by a kernel is linear over much of the grain filling period; under optimal conditions, N can accumulate at a rate of 0.03 to 0.04 mg kernel $^{-1}$ day $^{-1}$ (Sofield et al., 1977b). Enzymatic and structural protein constitutes most of the kernel's protein before the onset of rapid storage protein synthesis during the linear phase of grain filling. The synthesis of storage protein in the endosperm likely occurs on polyribosomes attached to endoplasmic reticulum. Following synthesis, protein accumulates within distended endoplasmic reticulum or vacuole-like structures (Campbell et al., 1981).

Examinations of the vascular system within the spikelet rachilla shows that kernels formed in distal florets are served by only a few, small vascular bundles that in turn are branches from larger bundles that link the proximal kernels to the vascular system of the rachis (Hanif and Langer, 1972; Simmons and Moss, 1978a). Such a vascular arrangement may favor assimilate transport to proximal kernels and help account for the differential growth patterns for kernels within a spikelet depicted in Fig. 3–5. However, kernel growth patterns within a spikelet are at least partly attributable to characteristics within the kernels themselves (Thornley et al., 1981).

Some research has addressed the processes by which sucrose and other assimilates accumulate in developing kernels as well as the possibility that a kernel's capacity to take up assimilates may itself limit yield. Lack of a positive correlation between kernel growth rates and intracellular endosperm sucrose concentrations has been interpreted to mean that kernel growth is determined primarily within the kernel itself, rather than by the availability of assimilates (Jenner and Rathjen, 1977, 1978).

Transfer cells exist at the insertion point of each kernel (Zee and O'Brien, 1971). There is no direct connection between the rachilla xylem and the xylem in the kernel (Zee and O'Brien, 1970), meaning that the phloem provides the only conduit for assimilate transport into the kernel. It is thought that solutes moving in the xylem are transferred to the phloem before moving into the kernel. Carbon is transported into the grain as sucrose, amides, and amino acids, the latter two of which also serve as the major transport forms for N (Donovan et al. 1983). A wide array of amino acid or amide N sources support grain growth when spikes are cultured in liquid media (Donovan and Lee, 1978; Singh and Jenner, 1983). These substances appear to enter the kernel by a common transport

mechanism. However, metabolism of amino acids within the vascular element may occur, whereas sucrose is not metabolized (Donovan et al., 1983).

Sucrose is thought to move out of the phloem of a kernel's vascular bundle and into the placental-chalazal region of the crease. It then diffuses across the endosperm cavity and into the intercellular space of the endosperm, from which it is taken up by individual endosperm cells (Chevalier and Lingle, 1983). Although activity of invertase and sucrose synthase, (two enzymes that catalyze sucrose hydrolysis) can be detected in the kernel during much of the grain-filling period, sucrose likely moves to the endosperm cells intact and is not cleaved during phloem unloading or subsequent transport across the endosperm (Sakri and Shannon, 1975; Jenner, 1974; Chevalier and Lingle, 1983).

Both UDP– and ADP-glucose pyrophosphorylase, which control synthesis of UDPG and ADPG, are present in the developing endosperm during the period of maximum grain starch synthesis (Kumar and Singh, 1980). However, ADPG is thought to provide most of the glucosyl residues for starch synthesis (Austin and Jones, 1975). The reaction catalyzed by ADPG-pyrophosphorylase may be rate-limiting in developing kernels (Kumar and Singh, 1980. Mengel and Judel (1981) proposed that starch phosphorylase, an enzyme which catalyzes the reaction of glucose-1-phosphate with a glucan polymer, may be important for starch synthesis early in grain filling when levels of glucose-1-P are relatively high. Later, starch synthase I (ADP-starch synthase) may be of greater importance for starch synthesis.

The movement of water into developing kernels is an enigma. About 14 days after anthesis the water content of a kernel attains a relatively constant level, despite the kernel's continued rapid increase in dry matter (Sofield et al., 1977b; Simmons and Crookston, 1979; Jenner, 1982). One-half to two-thirds of a kernel's final weight may accumulate without further increase in its water content (Jenner, 1982). Thus, either the dry matter moves into the grain without a corresponding influx of water, or water moving into the kernel with the dry matter is balanced by a corresponding efflux of water. In addressing these alternatives, Jenner (1982) postulates that solutes enter the kernel in the phloem as a bulk-flow of solution and that both solutes and water may be unloaded into the apoplast, although possibly not in proportional amounts. However, recirculation of water in a conduit separated from the apoplast of the kernel is also a possibility (Jenner, 1982).

At physiological maturity (maximum dry weight), water content of the kernels declines rapidly (Kirby and Appleyard, 1981; Sofield et al., 1977b) (Fig. 3–6). This stage often corresponds to a moisture percentage between 30 and 40%, although Hanft and Wych (1982) found moisture percentage per se to be an unreliable indicator of physiological maturity.

Changes in the anatomy of the chalazal region of the kernel's crease occur in association with the cessation of movement of dry matter, N,

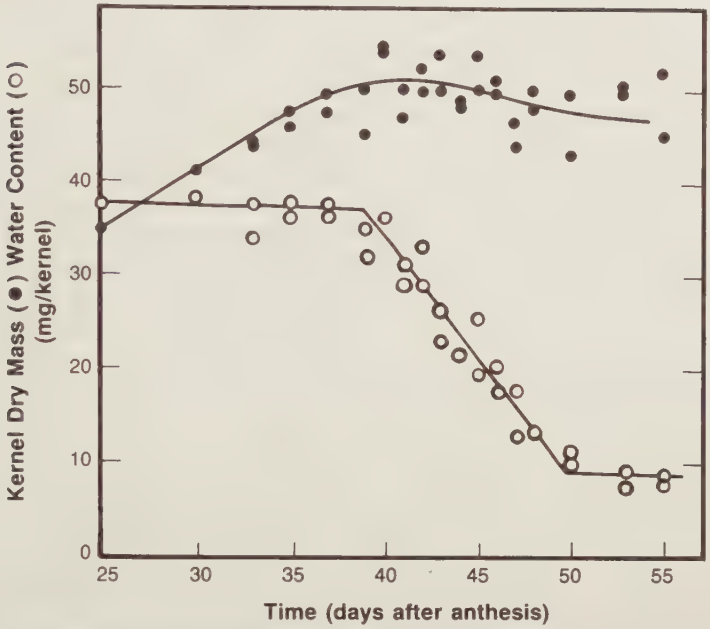

Fig. 3–6. Changes in dry matter (●) and water content (○) of first-floret kernels in centrally positioned spikelets of 'Triple Dirk' wheat (Sofield et al., 1977b).

P, and water into the kernel at physiological maturity (Sofield et al., 1977b). Deposition of polyphenolics within cells of the chalazal region of the kernel's crease begins about 2 weeks after anthesis (Cochrane, 1983). These are likely enclosed in membrane-bound bodies that later break down, causing cessation of symplastic movement of solutes through these cells. Near the end of the linear grain-filling phase a layer of suberin also is deposited outside the plasma membrane and the primary cell walls become lignified, thus reducing chalazal region apoplastic water and solute movement. Cochrane (1983) proposed a role for xylem parenchyma cells of the kernel's vascular element in promoting water loss from the endosperm after physiological maturity by an active mechanism. Similarly, premature lipid deposition in cells of the chalazal region occurs in response to water stress (Barlow et al., 1980).

Pre-harvest sprouting can be a problem when rains precede and delay harvest, particularly for white wheat (Hagemann and Ciha, 1984). Kernels that mature under cool conditions are more dormant than those ripened under warm conditions, but the physiological basis for this effect is not known (Austin and Jones, 1975).

Kernels contain plant hormones of varying abundance depending on the stage of development. Cytokinins tend to be most prevalent relatively early in the grain-filling period in association with rapid endosperm cell division. Cytokinin activity declines before the onset of rapid starch accumulation (Jameson et al., 1982). Abscisic acid content increases

throughout kernel development, reaching a peak near the end of grain filling. Later, as grain water content falls, ABA content also declines but levels of ABA metabolites increase (King, 1979). It is possible that ABA plays a role as an inhibitor of premature germination of the embryo. Gibberellin content increases rapidly during the period of starch synthesis and subsequently declines. Radley (1976) proposed that gibberellin is necessary to regulate growth of the various tissues of the caryopsis during the period of its rapid dry matter accumulation. Auxin content increases somewhat later than gibberellin (Radley, 1976), then declines when the kernels become capable of germination (Radley, 1979).

3–4 CARBON RELATIONSHIPS

3–4.1 Photosynthesis

Photosynthesis in wheat occurs via the C_3 scheme with carboxylation catalyzed by the enzyme ribulose bisphosphate carboxylase (rubisco). Although earlier optimism existed for finding a higher photosynthetic efficiency aberrant within the *Triticum* genus, it now appears that genotypes utilize the same basic mechanism (Moss, 1976).

Single leaf photosynthesis rates for controlled environment-grown plants usually approach light saturation at photon flux densities about one-third to one-half of full sunlight (Akita and Moss, 1973). However, wheat leaves developed under the higher radiation levels of the field may show less tendency to light saturate (Singh et al., 1974). The CO_2 compensation point is about 50 $\mu L\ L^{-1}$ (Moss et al., 1969). Photosynthetic rate response to temperature shows an optimum between 10 and 25°C (Evans et al., 1975). Normally, net photosynthetic rates in modern hexaploid genotypes will be about 0.6 to 1.2 mg $CO_2\ m^{-2}$ leaf area s^{-1}, but rates up to 1.9 mg $CO_2\ m^{-2}\ s^{-1}$ have been observed in wild diploid races (Austin and Jones, 1975).

The desirability of identifying genotypes possessing higher inherent rates of photosynthesis is evident, particularly since studies show that photosynthetic rate and biomass production of modern cultivars may be no better than in early cultivars or wild races (Evans and Dunstone, 1970; Austin et al., 1980). There are great practical difficulties in identifying superior photosynthetic genotypes (assuming that such exist). Measurements of photosynthesis at a single point in time have limited value for characterizing the photosynthetic performance of a genotype, since growing conditions, leaf position, leaf age, and rate of photoassimilate utilization can all influence the rates of photosynthesis observed (King et al., 1967; Osman and Milthorpe, 1971; Dantuma, 1973; Rawson et al., 1983). Furthermore, yield ultimately is influenced by other important characteristics of genotypes such as leaf area, partitioning of photoassimilates, and respiration. Thus, it remains to be seen whether wholesale screening for photosynthetic rate in breeding programs will be meaningful.

Assimilate production of individual leaves on wheat plants depends on the rate of photosynthesis, leaf area, and duration of leaf function. There is a general negative correlation between individual leaf area and photosynthetic rate across diploid, tetraploid, and hexaploid genetypes (Evans and Dunstone, 1970; Austin et al., 1982) and among hexaploid lines (Gale et al., 1974; Rawson et al., 1983). Photosynthetic trends over time for each leaf position on the plant are similar. Each leaf displays a photosynthetic plateau of variable duration followed by a decline as it senesces. Peak net photosynthesis per unit leaf area usually occurs after the leaf attains its maximum leaf area (after ligule emergence) (Rawson et al., 1983). The onset of the photosynthetic decline in leaves is hastened by shading, nutrient deficiency, or other stress conditions.

Canopy photosynthesis has been measured directly (Puckridge, 1971); Connor and Cartledge, 1971; Austin et al., 1976; Johnson et al., 1981), as well as estimated from individual leaf measurements (Rawson et al., 1983). Canopy photosynthesis generally follows the development and senescence patterns of the leaf area (Puckridge, 1971; Johnson et al., 1981). Canopy photosynthetic responses to increasing light do not exhibit the light saturation characteristics of individual leaves, but still tend to plateau at higher radiation intensities (Puckridge, 1971; Austin et al., 1976). The relation between radiation and canopy net photosynthesis depends on both the leaf area index and the canopy architecture, as well as the relative availability of other photosynthetic inputs such as CO_2 (Evans et al., 1975). During grain filling, most canopy leaf photosynthesis takes place in the top two or three leaves on the plant (Rawson et al., 1983).

A direct relationship between leaf photosynthesis and grain yield is not easy to demonstrate, although an abundance of indirect evidence from shading, thinning, and leaf area correlation studies (Simpson, 1968; Fischer, 1975; Fischer and Laing, 1976) implies that photosynthesis is important for yield. Difficulty in establishing a relationship between photosynthesis and yield results from the multitude of other factors that also influence yield. For example, an erect leaf genotype studied by Austin et al. (1976) was shown to have a higher canopy photosynthetic rate than a lax leaf genotype. It did not yield more, however, because the lax leaf line remobilized a greater quantity of material from the stems to the grain, which compensated for its lower supply of current photoassimilate. Data such as those of Fischer (1975) suggest that enhancing photosynthesis at critical times during the developmental cycle of the crop, such as during floret development, may be beneficial.

3–4.2 Partitioning of Photosynthate

In crop management, it is desirable to maintain functionality of the flag leaves throughout grain filling. Applications of protectant fungicides, for example, are often timed to correspond with appearance of these leaves. Early efforts to quantify the contributions of various photosyn-

thesizing plant organs to grain yield involved selective shading or defoliation treatments. These techniques can be misleading, however, since compensatory increases in photosynthesis by unshaded or remaining organs, or enhanced remobilization of earlier formed assimilates from vegetative organs may occur.

Direct measurements of CO_2 exchange of specific organs, coupled with ^{14}C-determined C partitioning patterns from those organs, are less equivocal. During vegetative development, photosynthate produced by early formed leaves is partitioned predominantly to emerging leaves, tillers, and roots (Doodson et al., 1964; Rawson and Hofstra, 1969). After jointing, intermediate level leaves in the canopy partition photosynthate extensively to the stem, with elongating internodes on either side of a leaf's node of attachment preferentially served by that leaf (Rawson and Hofstra, 1969; Patrick, 1972). Spike growth both before and after emergence from the boot is supported mostly by photosynthate from the upper two or three leaves on the plant (Rawson and Hofstra, 1969; Patrick, 1972).

Estimates suggest that from 70% to more than 90% of the grain yield is derived from photoassimilate produced after anthesis (Austin et al., 1977a; Bidinger et al., 1977). Judging by the relative photosynthetic activity of various organs during grain filling, the flag leaf blade and spike likely contribute the greatest quantities of photoassimilate to the grain. Specifically, the flag leaf blade may account for as much as 50% of the canopy phyotosynthate during early- and mid-grain filling (Austin and Jones, 1975; Rawson et al., 1983). Similarly, the spike and penultimate leaf blade may each contribute as much as 20% of the canopy photosynthate. Later in grain filling, the flag leaf sheath, penultimate leaf sheath, and peduncle together may contribute about 30% of the photosynthate at that time. Within a spike, the lemmas may contribute as much as 15% of the canopy photosynthesis during much of grain filling. Photosynthates from lemmas or glumes are translocated preferentially to their nearest kernels (Bremner and Rawson, 1972).

Precise estimates of the contributions of various photosynthesizing plant parts are difficult to obtain and likely vary with cultural conditions. Nevertheless the importance of maintaining photosynthetic capacity in the upper leaf blades, sheaths, and spike is evident. Awns can substantially increase the spike photosynthetic rate (Evans and Rawson, 1970; Teare et al., 1972). Awns may be particularly advantageous under drier cultural conditions, but they may also be neutral or disadvantageous in more humid conditions (McKenzie, 1972).

Harvest index has frequently been used as an indicator of overall partitioning efficiency for dry matter (Donald and Hamblin, 1976). As noted earlier, much of the recent gains in grain yield with modern wheat cultivars can be attributed to improvements in harvest index (Austin et al., 1980), which suggests that fundamental shifts in partitioning of photoassimilate have been achieved. Much of this proportional shift in dry

matter distribution in favor of grain has occurred in association with the development of semidwarf cultivars (Allan, 1983). Most semidwarf wheat cultivars grown commercially today possess only one of the major dwarfing genes, Rht_1 or Rht_2. Allan (1983) has shown that an additional increment in harvest index can be achieved with a two-gene dwarf. However, such genotypes have lower total biological and grain yields.

Austin et al. (1980) speculated that harvest index might ultimately be raised from the current 0.4 to 0.5 range to around 0.6. This might in itself increase grain yields approximately 30% above current levels. But considering that biological yield may be reduced by further shortening the stature of wheat, it may be that harvest index will need to be raised in some other fashion.

3–4.3 Translocation

Carbon assimilated by a mature leaf may be translocated immediately to another plant part, retained within the leaf, or respired soon after fixation. Ryle and Powell (1974) estimated that between 13 and 40% of the C assimilated by leaves of winter wheat is respired within 24 h.

The process and pathway by which photosynthate moves out of the chloroplasts, across leaf mesophyll and bundle sheath cells, and into the phloem has received considerable attention in some plant species (Giaquinta, 1983), but relatively little in wheat. However, wheat has served as a model system for investigating general characteristics of long distance translocation of assimilates. Wardlaw and Moncur (1976) showed that the requirement for assimilates by the spike influences the speed of movement of assimilates through the peduncle. Similarly, a reduction in the vascular tissue available for translocation causes increased velocities of ^{14}C assimilate and foliar-applied ^{32}P transport through the flag leaf sheath and peduncle (Marshall and Wardlaw, 1973).

Cook and Evans (1978, 1983) used surgically manipulated wheat plants to investigate the relative importance of sink size and distance from the assimilate source in determining partitioning patterns. Partitioning of ^{14}C to a sink was greatly influenced by the sink's relative size and proximity to the source, with the distance between source and sink playing a particularly important role. Factors such as hormonal influences (Patrick, 1976), vascular connections (Hanif and Langer, 1972; Whingwiri et al., 1981), and metabolic characteristics of the sink (Cook and Evans, 1983) may be important in establishing partitioning patterns.

3–4.4 Canopy Architecture

Photosynthesis may be affected, theoretically, by leaf posture and orientation. Erect leaf orientation should increase the penetration of light and increase the uniformity with which it is distributed within the crop canopy. It has been predicted that erect-leaf crops will have higher photosynthetic rates, particularly when leaf area indexes exceed 3 to 4 (Mon-

teith, 1965). Such conditions usually exist for a portion of the growing season before and after anthesis (Fig. 3–3). The photosynthetic advantage of erect leaves is expressed most during midday (Austin et al., 1976). Despite the apparent photosynthetic advantages of erect leaf canopy architecture, no studies have demonstrated a clear yield advantage for erect leaf plant types. Austin et al., (1976) demonstrated higher canopy photosynthesis rates and slower senescence of lower leaves for an erect-leaf genotype compared to a lax-leaf one. However, grain yields did not differ. Using a broader sampling of erect and lax-leaf lines, Innes and Blackwell (1983) also found little difference in grain yield. In some instances, however, biomass of the erect leaf lines appeared to be slightly higher. Unless deleterious influences of the erect-leaf character are found, it appears that it may be worthwhile for wheat, especially if cultural conditions have readily available moisture and promote high leaf area indexes during a major portion of the growing season (Innes and Blackwell, 1983).

Another aspect of canopy architecture is leaf twisting and curvature, both of which affect leaf orientation (Ledent and Moss, 1977). Both straight and curved flag leaves can be found within a single genotype, but genotype and N nutrition influence the proportion of straight or curved leaves in a canopy. Correlations between grain yield and leaf curvature have been inconclusive (Ledent and Renard, 1982).

3–4.5 Respiration

About half of the C assimilated during growth of a wheat plant is respired (King and Evans, 1976). This respiration is important for both synthesis of new material and maintenance of tissues. Rates of respiration at 25°C are only about 0.05 to 0.1 mg CO_2 m^{-2} s^{-1} (Austin and Jones, 1975). For each 10°C rise in temperature between 0 and 35°C, respiration rates nearly double (Austin and Jones, 1975).

Leaf or root respiration rates may be lower than those in the stem, particularly when the stem is elongating (Evans et al., 1975). Furthermore, respiration rates per unit of stem dry matter may be higher in some semidwarf genotypes (Rawson and Evans, 1971). Root respiration varies considerably, possibly because of differences in the supply of photosynthate translocated from shoots to roots over a day-night period (Osman, 1971).

Respiratory $^{14}CO_2$ loss from labeled plants is greatest within the first 12 hs after labeling and declines thereafter. The proportion of recently assimilated C lost to respiration is greatest for young plants and least for plants during the middle of grain filling (Morgan and Austin, 1983). Although respiration by kernels during grain filling may be great, adaptations such as the presence of phosphoenolpyruvate (PEP) carboxylase activity in the kernel pericarp (Wirth et al., 1977) may assist in refixing some of this respired C. Estimates of C refixation by spikes during mid-grain filling were much higher than for the plants as a whole at the same stage of growth (Morgan and Austin, 1983).

3–4.6 Assimilate Remobilization

Most dry matter contributing to grain yield is newly assimilated during grain filling, but conditions such as drought can occur where current assimilate supplies are reduced and the plants must rely on previously stored assimilates for grain filling (Gallagher et al., 1976). Bidinger et al. (1977) estimated that 13% of the grain yield in a well-watered wheat crop could be attributed to remobilization of preanthesis formed assimilates. The contribution increased to 27% under conditions of post-anthesis drought.

At least two sources of remobilized assimilates exist. First, high concentrations of soluble carbohydrates accumulate, particularly in stems, just before and after anthesis (Fig. 3–7). These are depleted during grain filling and a proportion are believed to be translocated to the grain (Wardlaw and Porter, 1967). In a sense, such carbohydrates represent a temporary store to meet the high demand for assimilates by kernels during

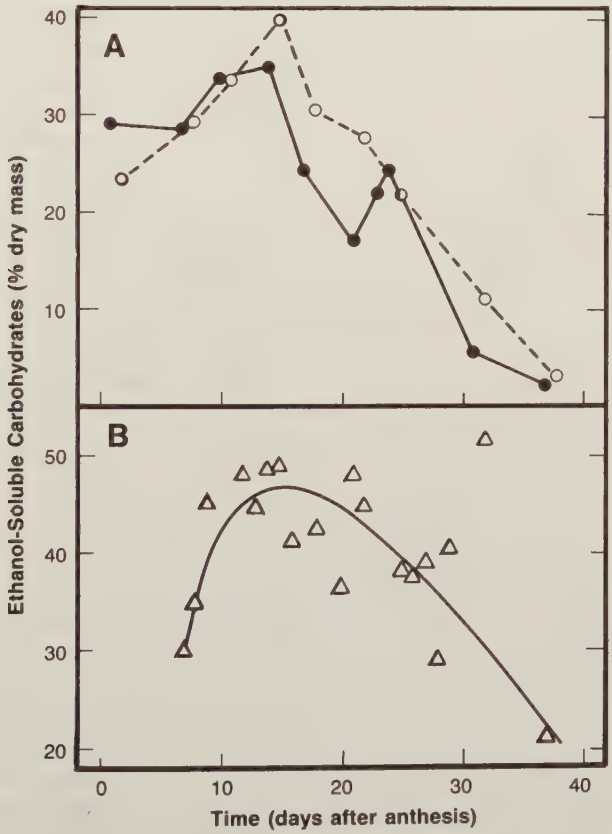

Fig. 3–7. Concentration of ethanol-soluble carbohydrates in stems during grain filling for two cultivars in 1976 (○, 'Maris Huntsman'; ●, 'Sportsman') and the cultivar Armada (△) in 1977 (Ford et al., 1979).

the linear phase of grain filling. Secondly, previously assimilated substances are remobilized from various vegetative plant parts as they senesce and are translocated to the grain. This latter mechanism provides much of the N for the developing grain. Estimates of the pre-anthesis assimilate contribution to grain yield (Bidinger et al., 1977), probably measure remobilized nitrogenous substances for the most part. Losses in stem dry matter commonly observed during grain filling include a sizeable loss due to respiration as well as assimilate remobilization to the grain (Austin et al., 1977a). Stem breakage before harvest can be associated with conditions that favor excessive mobilization and respiration of stem dry matter.

In a comparison of winter wheat genotypes differing in stem solidity, Ford et al. (1979) found no differences in either soluble carbohydrate concentrations in stems or absolute quantities of carbohydrate that they contained. Accordingly, solid-stemmed genotypes likely do not supply more remobilized carbohydrate to developing kernels than do normal hollow-stemmed ones. However, some variability in the soluble carbohydrate concentration of the stem exists among genotypes (Fig. 3–7), suggesting that genotypic differences in the capacity to store and remobilize carbohydrates also exist (Ford et al., 1979).

3–4.7 Senescence

Leaf area index of a wheat crop community reaches its peak before anthesis and then declines as leaf senescence progresses. Accordingly, senescence is a critical event in establishing the photosynthetic capacity of a crop. Grain yield may be positively related to the duration of leaf area (Evans et al., 1975). Environmental conditions such as moisture or N stress hasten senescence and reduce leaf area duration. An increase in yield is possible from CO_2 enrichment after anthesis (Krenzer and Moss, 1975; Fischer and Aguilar, 1976), suggesting that enhanced photosynthesis achieved through delayed canopy senescence might also increase grain yield.

Senescence has been studied intensively in an array of crops, but studies involving wheat plants senescing naturally under field conditions are less common (Patterson and Moss, 1979). Different characteristics of senescence are observed, depending on how an organ is induced to senesce. Furthermore, whether a senescing organ remains attached to the plant also has a bearing on its senescence characteristics (Patterson and Moss, 1979; Lazan et al., 1983).

The decline in photosynthetic activity of various plant organs or of the whole crop canopy during grain filling is associated with the onset of senescence (Patterson and Moss, 1979; Wittenbach, 1979). A loss of rubisco activity, the chief carboxylating enzyme in photosynthesis, is also associated with senescence (Hall et al., 1978; Wittenbach, 1979; Patterson et al., 1980; Peoples et al., 1980). Peoples et al. (1979) isolated several peptide hydrolases from wheat leaves that can degrade rubisco at a pH

at a pH optimum of around 5. The correspondence between the loss of rubisco protein and the loss of rubisco enzyme-specific activity is variable (Hall et al., 1978; Wittenbach, 1979; Peoples et al., 1980).

Defining the physiological trigger for senescence and possibly manipulating or delaying the senescence process have aroused considerable interest. It has become clear that senescence is a highly coordinated process, the specifics of which may vary depending on the conditions. Thus far, a primary induction event, if it exists, has not been identified. Lazan et al. (1983) proposed a role for the accumulation of carbohydrates in inducing senescence, but this would not seem to be important in tissues senescing because of prolonged darkness or an absence of CO_2.

Hormones have, of course, been proposed as a factor in crop senescence. A reduced cytokinin supply from the roots as grain filling progresses has been a persistent hypothesis regarding why senescence occurs in wheat. Published attempts to artificially manipulate senescence in the field through exogenous application of growth regulators, including cytokinins, have been largely unsuccessful (Hall et al., 1978); Patterson and Moss, 1979; Dybing and Lay, 1981). A role for the reproductive structures in senescence can be implied from experiments such as those of Patterson and Brun (1980), where premature removal of spikes delayed yellowing of upper leaves. However, the decline in rubisco activity in the de-spiked plants (normally associated with senescence) was not delayed, which casts doubt on whether functional senescence of the leaves was actually altered by the treatment.

3–5 NITROGEN RELATIONSHIPS

Although mineral nutrients other than N are important for wheat development and yield, N has received by far the most study. Sources such as Gasser and Thorburn (1972), Sofield et al. (1977b), Hill et al. (1978), Jensen (1978b), Gregory et al. (1979a, 1979b), and Mohamed and Marshall (1979) may be consulted for information concerning uptake and physiology of other nutrients in wheat.

3–5.1 Nitrogen Uptake from the Soil

Nutrient uptake depends on both a plant's inherent physiology and the nutrient's availability to the roots. This latter consideration is mostly a consequence of soil environmental conditions. Gregory et al. (1979b) demonstrated that crop growth rate was associated with N accumulation for winter wheat during the middle portion of the growing season for winter wheat. They interpreted these results as indicating that midseason crop demand determines uptake rate.

Under field conditions, without later applications of N fertilizers, N uptake is usually low following heading (Eilrich and Hageman, 1973; Austin et al., 1977b; Simmons and Moss, 1978b). However, under fa-

vorable post-anthesis conditions a large proportion of the final grain N can be derived from N taken up during grain filling (Evans et al., 1975). Genetic variation for N uptake characteristics during grain filling likely exists, but is difficult to quantify.

In the field, most N is absorbed as nitrate (NO_3^-) (Austin and Jones, 1975). Nitrate uptake by roots is probably carrier mediated. Nitrate-depleted seedlings grown in solution culture show an initial lag in NO_3^- uptake when first exposed to it (Ashley et al., 1975), suggesting that NO_3^- uptake and/or reduction mechanisms in the roots need to be induced before maximum uptake is possible.

Rooting characteristics such as depth, morphology, and duration of activity likely influence a plant's effectiveness in taking up N. However, rooting characteristics have been little studied, particularly in the field.

3–5.2 Nitrate Reduction

Once absorbed by the plant, NO_3^- must be reduced and combined with C before being utilized by the crop. Different pools of NO_3^- exist in plant cells, one readily available for reduction and a storage pool that is largely inaccessible to reduction. It is possible that vacuoles serve as a major storage pool for NO_3^- (Granstedt and Huffaker, 1982). Nitrate reduction can occur in either roots or shoots, but shoot reduction is probably more important quantitatively (Austin and Jones, 1975). The NO_3^-–induced enzyme, NO_3^- reductase, which catalyzes the reduction of NO_3^- to NO_2^-, has received considerable emphasis as a possible rate-limiting step in N nutrition of wheat (Beevers and Hageman, 1969; Eilrich and Hageman, 1973). Numerous attempts have been made to relate in vitro or in vivo NO_3^- reductase activities to N assimilation or grain protein characteristics, but with variable results. One difficulty is the inherent instability of NO_3^- reductase during extraction (Sherrard et al., 1979). Stability can be increased by inclusion of casein or bovine serum albumen (BSA) protein in the extraction medium (Sherrard and Dalling, 1978, 1979). Environmental and ontogenetically induced changes in activity are also observed (Croy and Hageman, 1970; Eilrich and Hageman, 1973; Dalling et al., 1975; Simmons and Moss, 1978b). Further, genotypes appear to differ in the apparent efficiency of their NO_3^- reductase enzyme by displaying differential relationships between NO_3^- reductase activity and total N accumulation (Dalling et al., 1975). Nevertheless, significant positive correlations between NO_3^- reductase activity and total plant reduced N have been observed (Eilrich and Hageman, 1973; Dalling et al., 1975). Correlations with grain protein yield or concentration, however, are more difficult to show. This is especially so if differences in N remobilization and redistribution patterns among genotypes are not taken into account (Dalling et al., 1975).

Deckard and Busch (1978) concluded that NO_3^- reductase activity values for an array of spring wheat genotypes were not well related to genotypic ability to assimilate N under field conditions. Conclusions of

Austin et al. (1978) concur with this assessment. On the other hand, some researchers are optimistic regarding the prospect of using NO_3^- reductase activity as a predictive indicator of crop yield or protein (Johnson et al., 1976; Dalling and Loyn, 1977; Blackwood and Hallam, 1979). Considering the total complexity of N assimilation by wheat in the field, with influences of both soil environmental and plant physiological factors, it is not surprising that such contrasting conclusions might be reached. However, it seems unlikely that NO_3^- reductase actually plays a rate-limiting role in N assimilation in the field, except perhaps at times during vegetative development when soil NO_3^- and moisture are readily available, or near the end of grain filling when NO_3^- reductase activities have declined to extremely low levels (Simmons and Moss, 1978b). Observation of NO_3^- in culms of spring wheat cultivars at maturity may indicate the need for enhanced NO_3^- reduction capacity during later stages of grain filling (Wych and Simmons, 1982).

Austin et al., (1977b) found a strong positive association between the accumulation of plant dry matter and the accumulation of N, both before and after anthesis. It may therefore be expedient to screen genotypes for high contents of reduced N. Austin et al. (1977b) cautioned that low straw weight genotypes may not accumulate enough N to sustain extremely high yields of high protein concentration grain.

3–5.3 Nitrogen Remobilization and Translocation

Earlier research concerning physiological factors influencing grain protein placed emphasis on N assimilation, and particularly NO_3^- reduction. Recently, relatively more attention has been given to understanding the processes and importance of N remobilization and redistribution within the plant. Dalling et al. (1975) highlighted the essentiality of linking efforts to increase N assimilation with a high efficiency of redistribution of previously assimilated N to the grain. Under usual field conditions, N in the grain is derived mainly from organic N present as components of vegetative plant parts and remobilized during grain filling. Wheat grown in controlled environments without an exogenous N supply after flag leaf emergence redistributes N extensively from vegetative plant parts to the grains. Leaves may contribute 40%, nongrain spike tissues 23%, the stem 23%, and roots 16% of the N moving to the grain during mid-grain filling (Simpson et al., 1983).

Studies under controlled environment conditions have examined N movements in wheat seedlings grown on a limited N supply (Simpson et al., 1982; Lambers et al., 1982). More than 50% of the daily N translocated to shoots was cycled back to the roots. This N exceeded the N nutrition needs of the roots and was transported back again to the shoot. It is thought that such cycling might occur repeatedly, indicating that N translocation and partitioning within vegetative plants may be very complex.

Not all genotypes necessarily translocate equal proportions of their

N to the grain (Dalling et al., 1975; Halloran and Lee, 1979; Halloran, 1981; Loffler and Busch, 1982). The extent to which N is remobilized by a particular genotype very much depends on the environmental conditions. The same genotype can exhibit extremely different N remobilization characteristics in different seasons (Wych and Simmons, 1982).

The extent of N remobilization in wheat has been most commonly expressed by means of the N harvest index, which is defined as the proportion of total aboveground plant N present in the grain. The concentration of N remaining in a vegetative plant part at maturity may also be a good indicator of how extensively N is mobilized from that plant part (Halloran and Lee, 1979).

The specific process whereby nitrogenous compounds are mobilized remains to be elucidated. Earlier studies established the importance of protein degradation in remobilization and implicated proteases in leaves as agents for catalyzing protein hydrolysis. Protease activity in leaves increases during grain filling, coincident with the decline in leaf N content (Rao and Croy, 1972; Dalling et al., 1976).

Although storage proteins, per se, do not exist in nongrain tissues, rubisco is an abundant leaf protein, and it has accordingly received attention as a likely major donor of organic N during remobilization. The initial loss of soluble protein from attached leaves during dark-induced senescence is almost entirely from rubisco (Wittenbach, 1978). Absolute content of rubisco in flag leaves during grain filling declines in approximate proportion to the loss of total soluble protein (Fig. 3–8). Proteolytic activity in the flag and penultimate leaves during grain filling, assayed using purified tobacco rubisco as a substrate rises gradually following anthesis and then rapidly reaches a peak at midsenescence (Wittenbach, 1979; Peoples et al., 1980).

In plants actively transporting mobilized N to the grain, glutamate, aspartate, serine, alanine, and glycine were the most prevalent amino acids present in flag leaf phloem exudate (Simpson and Dalling, 1981). Glutamine became a major phloem-translocated amino acid later in senescence and was the prominent amino acid in the xylem at all times.

Nitrogen translocated in the xylem apparently does not move directly into the grain, because of the discontinuous xylem at the base of a floret (Zee and O'Brien, 1970), but must transfer to the phloem for movement into the kernels. The leaves and glumes, as prominent organs for transpiration, probably serve as important points for xylem-to-phloem transfer of nitrogenous solutes (Simpson et al., 1983). Since transfer cells exist in the stem nodes in wheat (Hamilton and O'Brien, 1979), it is possible that these also are sites for such transfer. Amino acids transferred from the xylem may be converted before being loaded into the phloem (Simpson and Dalling, 1981). It is probable that a complex situation exists whereby some N moving in an organ such as a leaf via the xylem is transferred immediately to the phloem and translocated from the leaf, while other N is incorporated into the leaf amino acid pools or proteins and may be re-mobilized later.

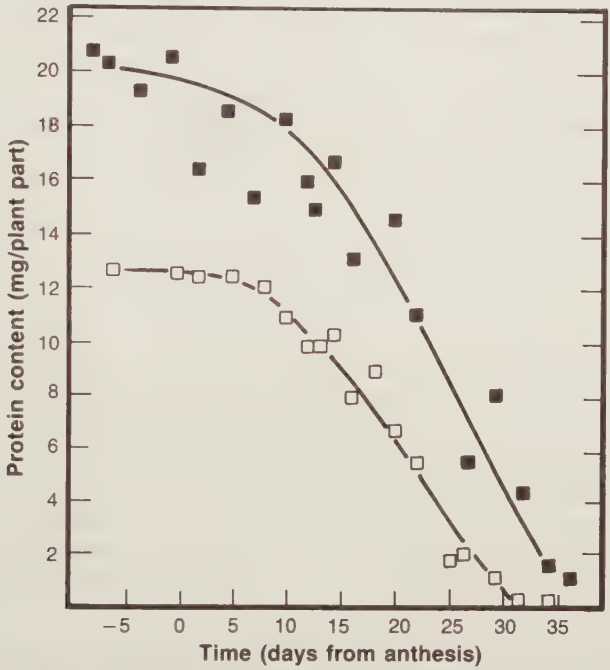

Fig. 3–8. Change in flag leaf content of rubisco protein (□) and total soluble protein (■) during grain filling and terminal senescence (Peoples et al., 1980).

Simpson et al. (1983) found that much of the N remobilized from leaves via the phloem during grain filling was translocated to the roots, rather than directly to the kernels. Some of this N was retranslocated to the shoot in the xylem. In agreement with this scheme, severing the phloem between the leaves and the spike did not seem to diminish the effective translocation of N to the grain (Martin, 1982). Thus, the situation for wheat during grain filling resembles that in vegetative plants where complex cycling of nitrogenous solutes from shoots to roots to shoots may occur.

It is not yet clear what possibilities exist for modifying the process of N remobilization. Using ^{15}N techniques, Rawson and Donald (1969) found that tertiary tillers remobilized 84% of their N to surviving shoots when they senesced under low N conditions. Some of the N remaining in vegetative plant parts at maturity makes up enzyme and structural proteins that are essential for the remobilization process itself and as such are not likely to be remobilized. However, some of the N remaining in vegetative tissues at maturity may be capable of being mobilized. As more is learned about the remobilization process, constraints to more extensive remobilization should be identified.

Peoples et al. (1980) made anatomical observations of ultrastructural changes of flag leaf cells during senescence. These bear on the question of N remobilization, since the maintenance of membrane integrity is

probably important for the membrane transport and compartmentation within cells associated with the N remobilization process. Plasma membranes were observed to remain stable throughout grain filling. Similarly, the tonoplasts appeared to maintain integrity well into flag leaf senescence. The integrity of organelles of the bundle sheath cells also seemed to be maintained late into senescence, a fact that is likely important for retaining the capacity to translocate solutes out of the leaf during mobilization.

3–6 CONCLUSIONS

Some wheat physiologists view the ultimate application of their discipline as the elimination or modification of specific characters that constrain crop productivity or quality. Achieving this goal should be possible as researchers develop deeper understanding of the physiology of wheat.

Studies designed to probe the physiological dynamics of yield in wheat have been conducted largely since the 1950s and 1960s. (Evans et al., 1975). Considering this relatively late start, it is not surprising that many studies have been directed at explaining what has already happened in the course of wheat improvement rather than at describing avenues for future improvement; this is a logical point at which to begin. Since the mid 1970s, however, physiological research has become less concerned with explaining past gains, and more with understanding the fundamental processes influencing grain yield or quality. Examples of this shift in focus include research examining the biochemical and physiological characteristics of kernel development and the dynamics of N re-mobilization and translocation.

Engledow and Wadham (1923) first articulated the need to identify an optimum plant form. Donald (1968) restated that goal by describing an ideotype for wheat. One element hindering achievement of this goal has been the complexity introduced by the need to specify the environmental conditions under which a particular plant design model would be favored. For example, remobilized assimilates are known to contribute to grain yield in direct proportion to the availability of current photosynthate during grain filling. Many nonirrigated locations experience great year-to-year variability in environmental conditions during grain filling. Thus, a physiologist faces a dilemma in specifying an optimum plant type for assimilate mobilization characteristics under such variable conditions.

Progress is being made in understanding wheat growth, development, and physiology. This review has concentrated on references published since the reviews by Evans et al. (1975) and Austin and Jones (1975). Many areas that needed research then still remain in need of more research, although advances have been made in understanding some topics, such as senescence, N assimilation, and kernel development. Some clear imperatives for future research are increasing the plant's inherent assim-

ilation capacity and understanding the fundamental physiological mechanisms governing photoassimilate partitioning.

REFERENCES

Akita, S., and D.N. Moss. 1973. Photosynthetic responses to CO_2 and light by maize and wheat leaves adjusted for constant stomatal apertures. Crop Sci. 13:234–237.

Allan, R.E. 1980. Influence of semidwarfism and genetic background on stand establishment of wheat. Crop Sci. 20:634–638.

----. 1983. Harvest indexes of backcross-derived wheat lines differing in culm height. Crop Sci. 23:1029–1032.

----, O.A. Vogel, and C.J. Peterson. 1962. Seedling emergence rate of fall sown wheat and its association with plant height and coleoptile length. Agron. J. 54:347–350.

Allison, J.C.S., and T.B. Daynard. 1976. Effect of photoperiod on development and number of spikelets of a temperate and some low-latitude wheats. Ann. Appl. Biol. 83:93–102.

Ashley, D.A., W.A. Jackson, and R.J. Vold. 1975. Nitrate uptake and assimilation by wheat seedlings during initial exposure to nitrate. Plant Physiol. 55:1102–1106.

Austenson, H.M., and P.D. Walton. 1970. Relationships between initial seed weight and mature plant characters in spring wheat. Can. J. Plant Sci. 50:53–58.

Austin, R.B. 1982. Crop characteristics and the potential yield of wheat. J. Agric. Sci. 98:447–453.

----, J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan, and M. Taylor. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci. 94:675–689.

----, J.A. Edrich, M.A. Ford, and R.D. Blackwell. 1977a. The fate of the dry matter, carbohydrates and ^{14}C lost from the leaves and stems of wheat during grain filling. Ann. Bot. 41:1309–1321.

----, M.A. Ford, J.A. Edrich, and R.D. Blackwell. 1977b. The nitrogen economy of winter wheat. J. Agric. Sci. 88:159–167.

----, ----, ----, and B.E. Hooper. 1976. Some effects of leaf posture on photosynthesis and yield in wheat. Ann. Appl. Biol. 83:425–446.

----, and H.G. Jones. 1975. The physiology of wheat. p. 20–73. *In* Plant Breeding Institute, Annual Report—1974. Cambridge, UK.

----, C.L. Morgan, M.A. Ford, and S.G. Bhaqwat. 1982. Flag leaf photosynthesis of *Triticum aestivum* and related diploid and tetraploid species. Ann. Bot. 49:177–189.

----, L. Rossi, and R.D. Blackwell. 1978. Relationships between nitrate reductase activity, plant weight and nitrogen content in seedlings of *Triticum*, *Aegilops*, and *Triticale*. Ann. Bot. 42:429–438.

Barlow, E.W.R., J.W. Lee, R. Munns, and M.G. Smart. 1980. Water relations of the developing wheat grain. Aust. J. Plant Physiol. 7:519–525.

Bauer, A., A.B. Frank, and A.L. Black. 1984. Estimation of spring wheat leaf growth rates and anthesis from air temperature. Agron. J. 76:829–835.

Beevers, L., and R.H. Hageman. 1969. Nitrate reduction in higher plants. Annu. Rev. Plant Physiol. 20:495–522.

Bhullar, S.S., and C.F. Jenner. 1983. Responses to brief periods of elevated temperature in ears and grains of wheat. Aust. J. Plant Physiol. 10:549–560.

Bidinger, F., R.B. Musgrave, and R.A. Fischer. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature (London) 270:431–433.

Blackwood, J.C., and R. Hallam. 1979. Nitrate reductase activity in wheat (*Triticum aestivum* L.) II. The correlation with yield. New Phytol. 82:417–425.

Bremner, P.M. 1972. Accumulation of dry matter and nitrogen by grains in different po-

sitions of the wheat ear as influenced by shading and defoliation. Aust. J. Biol. Sci. 25:657–668.

----, and J.L. Davidson. 1978. A study of grain number in two contrasting wheat cultivars. Aust. J. Agric. Res. 28:431–441.

----, and H.M. Rawson. 1972. Fixation of $^{14}CO_2$ by flowering and non-flowering glumes of the wheat ear, and the pattern of transport of label to individual grains. Aust. J. Biol. Sci. 25:921–930.

----, and ----. 1978. The weights of individual grains of the wheat ear in relation to their growth potential, the supply of assimilate and interaction between grains. Aust. J. Plant Physiol. 5:61–72.

Brocklehurst, P.A. 1977. Factors controlling grain weight in wheat. Nature (London) 266:348–349.

----, J.P. Moss, and W. Williams. 1978. Effects of irradiance and water supply on grain development in wheat. Ann. Appl. Biol. 90:265–276.

Brooking, I.R., and E.J.M. Kirby. 1981 Interrelationships between stem and ear development in winter wheat: the effects of a Norin 10 dwarfing gene, Gai/Rht$_2$. J. Agric. Sci. 97:373–381.

Campbell, W.P., J.W. Lee, T.P. O'Brien, and M.G. Smart. 1981. Endosperm morphology and protein body formation in developing wheat grain. Aust. J. Plant Physiol. 8:5–19.

Chevalier, P., and S.E. Lingle. 1983. Sugar metabolism in developing kernels of wheat and barley. Crop Sci. 23:272–277.

Cholick, F.A., J.R. Welsh, and C.V. Cole. 1977. Rooting patterns of semi-dwarf and tall winter wheat cultivars under dryland field conditions. Crop Sci. 17:637–639.

Cochrane, M.P. 1983. Morphology of the crease region in relation to assimilate uptake and water loss during caryopsis development in barley and wheat. Aust. J. Plant Physiol. 10:473–491.

Connor, P.J., and O. Cartledge. 1971. Structure and photosynthesis of wheat communities. J. Appl. Ecol. 8:469–475.

Cook, M.G., and L.T. Evans. 1978. Effect of relative size and distance of competing sinks on the distribution of photosynthetic assimilates in wheat. Aust. J. Plant Physiol. 5:495–509.

----, and ----. 1983. The roles of sink size and location in the partitioning of assimilates in wheat ears. Aust. J. Plant Physiol. 10:313–327.

Craig, S., and T.P. O'Brien. 1975. The lodicules of wheat: Pre-and post-anthesis. Aust. J. Bot. 23:451–458.

Croy, L.I., and R.H. Hageman. 1970. Relationship of nitrate reductase activity to grain protein production in wheat. Crop Sci. 10:280–285.

Dalling, M.J., G. Boland, and J.H. Wilson. 1976. Relation between acid proteinase activity and redistribution of nitrogen during grain development in wheat. Aust. J. Plant Physiol. 3:721–730.

----, G.M. Halloran, and J.H. Wilson. 1975. The relation between nitrate reductase activity and grain nitrogen productivity in wheat. Aust. J. Agric. Res. 26:1–10.

----, and R.H. Loyn. 1977. Level of activity of nitrate reductase at the seedling stage as a predictor of grain nitrogen yield in wheat (*Triticum aestivum* L.). Aust. J. Agric. Res. 28:1–4.

Dantuma, G. 1973. Rates of photosynthesis in leaves of wheat and barley varieties. Neth. J. Agric. Sci. 21:181–187.

Darwinkle, A. 1978. Patterns of tillering and grain production of winter wheat at a wide range of plant densities. Neth. J. Agric. Sci. 26:383–398.

Deckard, E.L., and R.H. Busch. 1978. Nitrate reductase assays as a prediction test for crosses and lines in spring wheat. Crop Sci. 18:289–293.

DeJong, R., and K.F. Best. 1979. The effect of soil water potential, temperature and seeding depth on seedling emergence of wheat. Can. J. Soil Sci. 59:259–264.

Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385–403.

----, and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agron. 28:361–405.

Donovan, G.R., C.F. Jenner, J.W. Lee, and P. Martin. 1983. Longitudinal transport of sucrose and amino acids in the wheat grain. Aust. J. Plant Physiol. 10:31–42.

----, and J.W. Lee. 1978. Effect of the nitrogen source on grain development in detached wheat heads in liquid culture. Aust. J. Plant Physiol. 5:81–87.

Doodson, J.K., J.G. Manners, and A. Myers. 1964. The distribution pattern of ^{14}Carbon assimilated by the third leaf of wheat. J. Exp. Bot. 15:96–103.

Dybing, C.D., and C. Lay. 1981. Yields and yield components of flax, soybean, wheat and oats treated with morphactins and other growth regulators for senescence delay. Crop Sci. 21:904–908.

Eilrich, G.L., and R.H. Hageman. 1973. Nitrate reductase activity and its relationship to accumulation of vegetative and grain nitrogen in wheat (*Triticum aestivum* L.). Crop Sci. 13:59–66.

Engledow, F.L., and S.M. Wadham. 1923. Investigations on yield in the cereals. Part I. J. Agric. Sci. 13:390–439.

Evans, L.T. 1980. The natural history of crop yield. Am. Sci. 68:388–397.

----, J. Bingham, and M.S. Roskams. 1972. The pattern of grain set within ears of wheat. Aust. J. Biol. Sci. 25:1–8.

----, and R.L. Dunstone. 1970. Some physiological aspects of evolution in wheat. Aust. J. Biol. Sci. 23:725–741.

----, and H.M. Rawson. 1970. Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. Aust. J. Biol. Sci. 23:245–254.

----, and I.F. Wardlaw. 1976. Aspects of the comparative physiology of grain yield in cereals. Adv. Agron. 28:301–359.

----, ----, and R.A. Fischer. 1975. Wheat. p. 101–149. *In* L.T. Evans (ed.) Crop physiology. Cambridge University Press, Cambridge.

Fischer, R.A. 1975. Yield potential in a dwarf spring wheat and the effect of shading. Crop Sci. 15:607–613.

----, and I. Aguilar M. 1976. Yield potential in a dwarf spring wheat and the effect of carbon dioxide fertilization. Agron. J. 68:749–752.

----, and D.R. Laing. 1976. Yield potential in a dwarf spring wheat and response to crop thinning. J. Agric. Sci. 87:113–122.

Ford, M.A., R.D. Blackwell, M.L. Parker, and R.B. Austin. 1979. Associations between stem solidity, soluble carbohydrate accumulation and other characters in wheat. Ann. Bot. 44:731–738.

Friend, D.J.C., V.A. Helson, and J.E. Fisher. 1962. Leaf growth in Marquis wheat as regulated by temperature, light intensity and daylength. Can. J. Bot. 40:1299–1311.

Gale, M.D., J.A. Edrich, and F.G.H. Lupton. 1974. Photosynthetic rates and the effects of applied gibberellin in some dwarf, semi-dwarf and tall wheat varieties (*Triticum aestivum*). J. Agric. Sci. 83:43–46.

Gallagher, J.N., P.V. Biscoe, and B. Hunter. 1976. Effects of drought on grain growth. Nature (London) 264:541–542.

Gasser, J.K.R., and M.A.P. Thorburn. 1972. The growth, composition and nutrient uptake of spring wheat. Effects of fertilizer N, irrigation and CCC on dry matter and N, P, K, Ca, Mg, and Na. J. Agric. Sci. 78:393–404.

Giaquinta, R.T. 1983. Phloem loading of sucrose. Annu. Rev. Plant Physiol. 34:347–387.

Granstedt, R.C., and R.C. Huffaker. 1982. Identification of the leaf vacuole as a major nitrate storage pool. Plant Physiol. 70:410–413.

Gregory, P.J., D.V. Crawford, and M. McGowan. 1979a. Nutrient relations of winter wheat. I. Accumulation and distribution of Na, K, Ca, Mg, P, S, and N. J. Agric. Sci. 93:485–494.

----, ----, and ----. 1979b. Nutrient relations of winter wheat. II. Movement of nutrients to the root and their uptake. J. Agric. Sci. 93:495–504.

Hadjichristodoulou, A., A. Della, and J. Photiades. 1977. Effect of sowing depth on plant establishment, tillering capacity and other agronomic characters of cereals. J. Agric. Sci. 89:161–167.

Hagemann, M.G., and A.J. Ciha. 1984. Evaluation of methods used in testing winter wheat susceptibility to preharvest sprouting. Crop Sci. 24:249–254.

Hall, N.P., A.J. Keys, and M.J. Merrett. 1978. Ribulose 1, 5-diphosphate carboxylase protein during flag leaf senescence. J. Exp. Bot. 29:31–37.

Halloran, G.M. 1981. Cultivar differences in nitrogen translocation in wheat. Aust. J. Agric. Res. 32:535–544.

----, and J.W. Lee. 1979. Plant nitrogen distribution in wheat cultivars. Aust. J. Agric. Res. 30:779–789.

Hamilton, B.C., and T.P. O'Brien. 1979. Aspects of vascular anatomy and differentiation of vascular tissues and transfer cells in vegetative nodes of wheat. Aust. J. Bot. 27:703–711.

Hanft, J.M., and R.D. Wych. 1982. Visual indicators of physiological maturity of hard red spring wheat. Crop Sci. 22:584–588.

Hanif, M., and R.J.M. Langer. 1972. The vascular system of the spikelet in wheat (*Triticum aestivum*). Ann. Bot. 36:721–727.

Harlan, J.R. 1975. Crops and man. American Society of Agronomy and Crop Science Society of America, Madison, WI.

Hill, J., A.D. Robson, and J.F. Loneragan. 1978. The effects of copper and nitrogen supply on the retranslocation of copper in four cultivars of wheat. Aust. J. Agric. Res. 29:925–939.

Houseley, T.L., A.W. Kirleis, H.W. Ohm, and F.L. Patterson. 1982. Dry matter accumulation in soft red winter wheat seeds. Crop Sci. 22:290–294.

Innes, P., and R.D. Blackwell. 1983. Some effects of leaf posture on the yield and water economy of winter wheat. J. Agric. Sci. 101:367–376.

----, ----, R.B. Austin, and M.A. Ford. 1981. The effects of selection for number of ears on the yield and water economy of winter wheat. J. Agric. Sci. 97:523–532.

Ishag, H.M., and M.B. Taha. 1974. Production and survival of tillers of wheat and their contribution to yield. J. Agric. Sci. 83:117–124.

Jameson, P.E., J.A. McWha, and G.J. Wright. 1982. Cytokinins and changes in their activity during the development of grains of wheat (*Triticum aestivum* L.). Z. Pflanzenphysiol. 106:27–36.

Jenner, C.F. 1974. An investigation of the association between the hydrolysis of sucrose and its absorption by grains of wheat. Aust. J. Plant Physiol. 1:319–329.

----. 1979. Grain-filling in wheat plants shaded for brief periods after anthesis. Aust. J. Plant Physiol. 6:629–641.

----. 1980. Effects of shading or removing spikelets in wheat: Testing assumptions. Aust. J. Plant Physiol. 7:113–121.

----. 1982. Movement of water and mass transfer into developing grains of wheat. Aust. J. Plant Physiol. 9:69–82.

----, and A.J. Rathjen. 1977. Supply of sucrose and its metabolism in developing grains of wheat. Aust. J. Plant Physiol. 4:691–701.

----, and ----. 1978. Physiological basis of genetic differences in the growth of grains of six varieties of wheat. Aust. J. Plant Physiol. 5:249–262.

Jensen, N.F. 1978a. Limits to growth in world food production. Science 201:317–320.

Jensen, P. 1978b. Changes in ion transport in spring wheat during ontogenesis. Physiol. Plant. 43:129–135.

Johnson, C.B., W.J. Whittington, and G.C. Blackwood. 1976. Nitrate reductase as a possible predictive test of crop yield. Nature (London) 262:133–134.

Johnson, R.C., R.E. Witters, and A.J. Ciha. 1981. Apparent photosynthesis, evapotranspiration, and light penetration in two contrasting hard red winter wheat canopies. Agron. J. 73:419–422.

Kemp, D.R., and W.M. Blacklow. 1982. The responsiveness to temperature of the extension rates of leaves of wheat growing in the field under different levels of nitrogen fertilizer. J. Exp. Bot. 33:29–36.

Kettlewell, P.S., E.A. Whitley, W.S. Meredith, and R. Sylvester-Bradley. 1983. Effects of early application of chlormequat on tillering and yield of winter wheat. J. Agric. Sci. 100:735–738.

King, R.W. 1979. Abscisic acid synthesis and metabolism in wheat ears. Aust. J. Plant Physiol. 6:99–108.

----, and L.T. Evans. 1967. Photosynthesis in artificial communities of wheat, lucerne and subterranean clover plants. Aust. J. Biol. Sci. 20:623–635.

----, I.F. Wardlaw, and L.T. Evans. 1967. Effect of assimilate utilization on photosynthetic rate in wheat. Planta 77:261–276.

Kirby, E.J.M. 1974. Ear development in spring wheat. J. Agric. Sci. 82:437–447.

----. 1983. Development of the cereal plant. pp. 1–3. *In* D.W. Wright (ed.) The yield of cereals. Royal Agriculture Society of England, London.

----, and M. Appleyard. 1981. Cereal development guide. National Agricultural Center Cereal Unit, Stoneleigh, UK.

----, and ----, and G. Fellowes. 1983. Plant development: Leaf emergence and tillering in wheat. p. 114–116. *In* Plant Breeding Institute, Annual Report—1982. Cambridge, UK.

Kishitani, S., and S. Tsunoda. 1981. Physiological aspects of domestication in diploid wheat. Euphytica 30:247–252.

Klepper, B., R.K. Belford, and R.W. Rickman. 1984. Root and shoot development in winter wheat. Crop Sci. 76:117–122.

Krenzer, E.G., and D.N. Moss. 1975. Carbon dioxide enrichment effects upon yield and yield components in wheat. Crop Sci. 15:71–74.

Kumar, R., and R. Singh. 1980. The relationship of starch metabolism to grain size in wheat. Phytochemistry 19:2299–2303.

Lambers, H., R.J. Simpson, V.C. Beilharz, and M.J. Dalling. 1982. Growth and translocation of C and N in wheat (*Triticum aestivum*) grown with a split root system. Physiol. Plant. 56:421–429.

Langer, R.H.M., and C.T. Dougherty. 1976. Physiology of grain yield in wheat. pp. 59–67. *In* N. Sunderland (ed.) Perspectives in experimental biology. Vol. 2 (Botany). Pergamon, Oxford, UK.

Lazan, H.B., E.W.R. Barlow, and C.J. Brady. 1983. The significance of vascular connection in regulating senescence of the detached flag leaf of wheat. J. Exp. Bot. 34:726–736.

Ledent, J.F., and D.N. Moss. 1977. Spatial orientation of wheat leaves. Crop Sci. 17:873–879.

----, and C.H. Renard. 1982. Factors determining flag leaf curvature in wheat. Crop Sci. 22:617–622.

Lindstrom, M.J., R.I. Papendick, and F.E. Koehler. 1976. A model to predict winter wheat emergence as affected by soil temperature, water potential, and depth of planting. Agron. J. 68:137–141.

Loffler, C.M., and R.H. Busch. 1982. Selection for grain protein, grain yield, and nitrogen partitioning efficiency in hard red spring wheat. Crop Sci. 22:591–595.

Lowe, L.B., and S.K. Ries. 1972. Effects of environment on the relation between seed protein and seedling vigor in wheat. Can. J. Plant Sci. 52:157–164.

Lupton, F.G.H., R.H. Oliver, F.B. Ellis, B.T. Barnes, K.R. Howse, P.J. Welbank, and P.J. Taylor. 1974. Root and shoot growth of semi-dwarf and taller winter wheats. Ann. Appl. Biol. 77:129–144.

----, and M.J. Pinthus. 1969. Carbohydrate translocation from small tillers to spike producing shoots in wheat. Nature (London) 221:483–484.

MacKey, J. 1973. The wheat root. p. 827–842. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Marshall, C., and I.F. Wardlaw. 1973. A comparative study of the distribution and speed of movement of ^{14}C assimilates and foliar-applied ^{32}P-labelled phosphate in wheat. Aust. J. Biol. Sci. 26:1–13.

Martin, P. 1982. Stem xylem as a possible pathway for mineral retranslocation from senescing leaves to the ear in wheat. Aust. J. Plant Physiol. 9:197–207.

Martinez-Carrasco, R., and G.N. Thorne. 1979. Physiological factor limiting grain size in wheat. J. Exp. Bot. 30:669–679.

Masle-Meynard, J. 1981. Elaboration of the ears number of a winter wheat submitted to competition for nitrogen. I. Importance of a critical stage for a tiller, relevant to its elongation. Agronomie 1:623–632.

----, and M. Sebillotte. 1981. Study on the heterogeneity of a wheat stand. Study on the different sorts of individuals of the stand; factors allowing the description of its structure. Agronomie 1:217–224.

McKenzie, H. 1972. Adverse influence of awns on yield of wheat. Can. J. Plant Sci. 52:81–87.

Mengel, K., and G. Klaus Judel. 1981. Effect of light intensity on the activity of starch synthesizing enzymes and starch synthesis in developing wheat grains. Physiol. Plant. 51:13–18.

Mohamed, G.E.S., and C. Marshall. 1979. The pattern of distribution of phosphorus and dry matter with time in spring wheat. Ann. Bot. 44:721–730.

Mohapatra, P.K., D. Aspinall, and C.F. Jenner. 1982. The growth and development of the wheat apex: The effects of photoperiod on spikelet production and sucrose concentration in the apex. Ann. Bot. 49:619–626.

Monteith, J.L. 1965. Light distribution and photosynthesis in field crops. Ann. Bot. 29:17–37.

Morgan, C.L., and R.B. Austin. 1983. Respiratory loss of recently assimilated carbon in wheat. Ann. Bot. 51:85–95.

Moss, D.N. 1976. Studies on increasing photosynthesis in crop plants. p. 31–41. *In* R.H. Burris and C.C. Black (ed.) CO_2 metabolism and plant productivity. University Park Press, Baltimore, MD.

----, E.G. Krenzer, and W.A. Brun. 1969. Carbon dioxide compensation points in related plant species. Science 164:167–168.

Osman, A.M. 1971. Root respiration of wheat plants as influenced by age, temperature, and irradiance of shoots. Photosynthetica 5:107–112.

----, and F.L. Milthorpe. 1971. Photosynthesis of wheat leaves in relation to age, illuminance and nutrient supply. II. Results. Photosynthetica 5:61–70.

Patrick, J.W. 1972. Distribution of assimilate during stem elongation in wheat. Aust. J. Biol. Sci. 25:455–467.

----, 1976. Hormone-directed transport of metabolites. p. 433–446. *In* I.F. Wardlaw and J.B. Passioura (ed.) Transport and transfer processes in plants. Academic Press, New York.

Patterson, T.G., and W.A. Brun. 1980. Influence of sink removal in the senescence pattern of wheat. Crop Sci. 20:19–23.

----, and D.N. Moss. 1979. Senescence in field-grown wheat. Crop Sci. 19:635–640.

----, ----, and W.A. Brun. 1980. Enzymatic changes during the senescence of field-grown wheat. Crop Sci. 20:15–18.

Peoples, M.B., V.C. Beilharz, S.P. Waters, R.J. Simpson, and M.J. Dalling. 1980. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). Planta 149:241–251.

----, G.J.T. Frith, and M.J. Dalling. 1979. Proteolytic enzymes in green wheat leaves. IV. Degradation of ribulose 1, 5-bisphosphate carboxylase by acid proteinases isolated on DEAE-cellulose. Plant Cell Physiol. 20:253–258.

Peterson, C.M., B. Klepper, and R.W. Rickman. 1982. Tiller development at the coleoptilar node in winter wheat. Agron. J. 74:781–784.

Power, J.F., and J. Alessi. 1978. Tiller development and yield of standard and semi-dwarf spring wheat varieties as affected by nitrogen fertilizer. J. Agric. Sci. 90:97–108.

Puckridge, D.W. 1971. Photosynthesis of wheat under field conditions. III. Seasonal trends in carbon dioxide uptake of crop communities. Aust. J. Agric. Res. 22:1–9.

Radley, M. 1976. The development of wheat grain in relation to endogenous growth substances. J. Exp. Bot. 27:1009–1021.

Radley, M. 1979. The role of gibberellin, abscisic acid, and auxin in the regulation of developing wheat grains. J. Exp. Bot. 30:381–389.

----. 1980. Effect of abscisic and gibberellic acid on grain set in wheat. Ann. Appl. Biol. 95:409–414.

----, and G.N. Thorne. 1981. Effects of decreasing the number of grains in ears of cvs. Hobbit and Maris Huntsman winter wheat. Ann. Appl. Biol. 98:149–156.

Rahman, M.S., and J.H. Wilson. 1978. Determination of spikelet number in wheat. III. Effect of varying temperature on ear development. Aust. J. Agric. Res. 29:459–467.

Rao, S.C., and L.I. Croy. 1972. Protease and nitrate reductase seasonal patterns and their relation to grain production of 'high' versus 'low' protein wheat varieties. J. Agric. Food Chem. 20:1138–1141.

Rawson, H.M. 1971a. An upper limit for spikelet number per ear in wheat, as controlled by photoperiod. Aust. J. Agric. Res. 22:537–546.

----. 1971b. Tillering patterns in wheat with special reference to the shoot at the coleoptile node. Aust. J. Biol. Sci. 24:829–841.

----, and C.M. Donald. 1969. The absorption and distribution of nitrogen, after floret initiation in wheat. Aust. J. Agric. Res. 20:799–808.

----, and L.T. Evans. 1970. The pattern of grain growth within the ear of wheat. Aust. J. Biol. Sci. 23:753–764.

----, and ----. 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. Aust. J. Agric. Res. 22:851–863.

----, and G. Hofstra. 1969. Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of the wheat plant. Aust. J. Biol. Sci. 22:321–331.

----, J.H. Hindmarsh, R.A. Fischer, and Y.M. Stockman. 1983. Changes in leaf photosynthesis with plant ontogeny and relationships with yield per ear in wheat cultivars and 120 progeny. Aust. J. Plant Physiol. 10:503–514.

Rickman, R.W., B.L. Klepper and C.M. Peterson. 1983. Time distributions for describing appearance of specific culms of winter wheat. Agron. J. 75:551–556.

Ryle, G.J.A., and C.E. Powell. 1974. The utilization of recently assimilated carbon in graminaceous plants. Ann. Appl. Biol. 77:145–158.

Sakri, F.A.K., and J.C. Shannon. 1975. Movement of ^{14}C- labeled sugars in kernels of wheat (*Triticum aestivum* L.). Plant Physiol. 55:881–889.

Scott, W.R., C.T. Dougherty, and R.H.M. Langer. 1975. An analysis of a wheat yield depression caused by high sowing rate with reference to the pattern of grain set within the ear. N.Z. J. Agric. Res. 18:209–214.

Sherrard, J.H. and M.J. Dalling. 1978. Effect of casein on the extractability and stability of nitrate reductase from wheat leaves. Ann. Bot. 42:1421–1427.

----, and ----. 1979. *In vitro* stability of nitrate reductase from wheat leaves. I. Purification of nitrate reductase and its effect on stability. Plant Physiol. 63:346–353.

----, J.A. Kennedy, and M.J. Dalling. 1979. *In vitro* stability of nitrate reductase from wheat leaves. Plant Physiol. 64:439–444.

Simmons, S.R., and R.H. Busch. 1984. Kernel weight and growth rate responses to reductions in kernel number for spring wheat genotypes differing in kernel weight. Agron. Abstr. American Society of Agronomy, Madison, WI, p. 115.

----, and R.K. Crookston. 1979. Rate and duration of growth of kernels formed at specific florets in spikelets of spring wheat. Crop Sci. 19:690–693.

----, ----, and J.E. Kurle. 1982. Growth of spring wheat kernels as influenced by reduced kernel number per spike and defoliation. Crop Sci. 22:983–988.

----, and D.N. Moss. 1978a. Nitrogen and dry matter accumulation by kernels formed at specific florets in spikelets of spring wheat. Crop Sci. 18:139–143.

----, and ----. 1978b. Nitrate reductase as a factor affecting N assimilation during the grain filling period in spring wheat. Crop Sci. 18:584–586.

Simons, R.G. 1982. Tiller and ear production of winter wheat. Field Crop Abstr. 35:857–870.

----, and L.A. Hunt. 1983. Ear and tiller number in relation to yield in a wide range of genotypes of winter wheat. Z. Pflanzenzuecht. 90:249–258.

Simpson, G.M. 1968. Association between grain yield per plant and photosynthetic area above the flag-leaf node in wheat. Can. J. Plant Sci. 48:253–260.

Simpson, R.J., and M.J. Dalling. 1981. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.) III. Enzymology and transport of amino acids from senescing flag leaves. Planta 151:447–456.

----, H. Lambers, and M.J. Dalling. 1982. Translocation of nitrogen in a vegetative wheat plant (*Triticum aestivum* L.). Physiol. Plant. 56:11–17.

----, ----, and ----. 1983. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). Plant Physiol. 71:7–14.

Singh, B.K. and C.F. Jenner. 1982. Association between concentrations of organic nutrients in the grain, endosperm cell number and grain dry weight within the ear of wheat. Aust. J. Plant Physiol. 9:83–95.

----, and ----. 1983. Culture of detached ears of wheat in liquid culture: Modification and extension of the method. Aust. J. Plant Physiol. 10:227–236.

Singh, M., W.L. Ogren and J.M. Widholm. 1974. Photosynthetic characteristics of several C_3 and C_4 plant species grown under different light intensities. Crop Sci. 14:563–566.

Singh, M.K., and S. Tsunoda. 1978. Photosynthetic and transpirational response of a cultivated and a wild species of *Triticum* to soil moisture and air humidity. Photosynthetica 12:280–283.

Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977a. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4:785–797.

----, I.F. Wardlaw, L.T. Evans, and S.Y. Zee. 1977b. Nitrogen, phosphorus and water contents during grain development and maturation in wheat. Aust. J. Plant Physiol. 4:799–810.

Spiertz, J.H.J., and J. Ellen. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. Neth. J. Agric. Sci. 26:210–231.

Stern, W.R., and E.J.M. Kirby. 1979. Primordium initiation at the shoot apex in four contrasting varieties of spring wheat in response to sowing date. J. Agric. Sci. 93:203–215.

Stockman, Y.M., R.A. Fischer, and E.G. Brittain. 1983. Assimilate supply and floret development within the spike of wheat (*Triticum aestivum* L.) Aust. J. Plant Physiol. 10:585–594.

Teare, I.D., J.W. Sij, R.P. Waldren, and S.M. Goltz. 1972. Comparative data on the rate of photosynthesis, respiration and transpiration of different organs in awned and awnless isogenic lines of wheat. Can. J. Plant Sci. 52:965–971.

Thorne, G.N. 1981. Effects on dry weight and nitrogen content of grains of semi-dwarf and tall varieties of winter wheat caused by decreasing the number of grains per ear. Ann. Appl. Biol. 98:355–363.

Thornley, J.H.M., R.M. Gifford, and P.M. Bremner. 1981. The wheat spikelet—growth response to light and temperature—Experiment and hypothesis. Ann. Bot. 47:713–725.

Wardlaw, I.F. 1970. The early stages of grain development in wheat: Response to light and temperature in a single variety. Aust. J. Biol. Sci. 23:765–774.

----. 1971. The early stages of grain development in wheat: response to water stress in a single variety. Aust. J. Biol. Sci. 24:1047–1055.

----, and L. Moncur. 1976. Source, sink and hormonal control of translocation in wheat. Planta 128:93–100.

----, and H.K. Porter. 1967. The redistribution of stem sugars in wheat during grain development. Aust. J. Biol. Sci. 20:309–318.

----, I. Sofield, and P.M. Cartwright. 1980. Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. Aust. J. Plant Physiol. 7:387–400.

Whingwiri, E.E., J. Kuo, and W.R. Stern. 1981. The vascular system in the rachis of a wheat ear. Ann. Bot. 48:189–201.

Williams, R.F., and R.H.M. Langer. 1975. Growth and development of the wheat tiller. II. The dynamics of tiller growth. Aust. J. Bot. 23:745–759

Wirth, E., G.J. Kelley, G. Fischbeck, and E. Latzko. 1977. Enzyme activities and products of CO_2 fixation in various photosynthetic organs of wheat and oat. Z. Pflanzenphysiol. 82:78–87.

Wittenbach, V.A. 1978. Breakdown of ribulose bisphosphate carboxylase and change in proteolytic activity during dark-induced senescence of wheat seedlings. Plant Physiol. 62:604–608.

----. 1979. Ribulose bisphosphate carboxylase and proteolytic activity in wheat leaves from anthesis through senescence. Plant Physiol. 64:884–887.

Wych, R.D., and S.R. Simmons. 1982. Nitrogen partitioning in spring wheat genotypes differing in grain protein. Agron. Abstr. American Society of Agronomy, Madison, WI, p. 114.

Zee, S.Y., and T.P. O'Brien. 1970. A special type of tracheary element associated with 'xylem discontinuity' in the floral axis of wheat. Aust. J. Biol. Sci. 23:783–791.

----, and ----. 1971. Vascular transfer cells in the wheat spikelet. Aust. J. Biol. 24:35–49.

Zohary, D., J.R. Harlan, and A. Vardi. 1969. The wild diploid progenitors of wheat and their breeding value. Euphytica 18:58–65.

4 The Physiology of Water and Temperature Stress

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In developing cultivars for a particular climatic environment the breeder must make a choice between breeding for high yield potential or stability of yields. Under ideal growing conditions certain cultivars produce high yields, but they may be sensitive to stress conditions. Since a crop cultivar is grown under varying environmental conditions, the ability to adapt quickly to stress is an important aspect of its genetic make-up. However, stable lines often have low yields and genotype × environment interactions are usually evident only in the more extreme environments, which are not randomly distributed with respect to intensity or frequency (Fox and Rosielle, 1982.

Environmental stresses due to water or temperature extremes not only result in significant yield losses, but also prevent extension of a crop into new cropping areas. Boyer (1982) emphasized that under ideal conditions, yields five to seven times greater than average are possible. Therefore, the genetic potential for high yield is already present in many cultivars. What is lacking is *yield stability* i.e., the ability to produce high relative yields under conditions of stress. Improvement in crop management techniques could maximize the expression of genetic resistance to environmental stress. One example is the seeding of winter wheat into standing stubble, which traps snow and modifies the soil temperature at crown depth. This practice has allowed northward expansion of winter wheat in the Great Plains region of North America.

The response of a plant to a stress depends on its genetic potential to adapt, the duration of exposure, and stage of growth. For example, a

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drought stress generally occurs over a long period of time (days) before there is any effect on yield. Heat stress generally results in suppressed growth and reduced yield, but is rarely lethal. Freezing can also reduce yield and seed quality, and is more dramatic in that injury occurs in a matter of seconds if the plant is cooled below its critical temperature. Depending on the stage of development, yield can be reduced to zero.

This chapter describes the effects of subzero temperature, high temperature, and drought stresses on the physiology of the wheat plant. It discusses how wheat plants are thought to be injured by the stress and how wheat has evolved to adapt to these stresses.

4–1 FROST RESISTANCE

In 1936, Harrington (1936) cautioned that attempts to introduce disease resistance or other desirable traits into wheat may reduce its frost resistance. Recently Marcellos and Burke (1979) demonstrated that leaves of several unhardened spring wheat cultivars are able to tolerate −7 to −9 °C. Leaves of spring wheat 'Kite', 'Manitou', and 'Oxley' in the hardened state tolerated −9 to −10 °C before injury became apparent. The leaves of 'Norstar' and 'Cheyenne' winter wheats can tolerate −18 and −12 °C, respectively, when cold hardened (Chen et al., 1983; Marcellos and Burke, 1979). Gusta (unpublished observations) observed that leaves of field-grown 'Columbus' and 'Neepawa' wheat collected from mid- to late July survived temperatures as low as −8 °C. Temperatures at the time of collection were between 25 to 30 °C, indicating that the leaves possess considerable frost tolerance in the absence of hardening conditions. However, as the plants matured, the leaves could only tolerate −4 to −6 °C.

Although the leaves of wheat plants may possess a considerable degree of frost tolerance, the reproductive tissues of the developing ear are considerably less resistant to freezing and may be injured at −1.8 °C (Single and Marcellos, 1974). The floral parts within the flag leaf sheath may avoid freezing by supercooling, even though the rest of the plant is frozen. This is due to the inability of the ice front to travel across the node of the stem or rachis to the developing ear (Single and Marcellos, 1974). Ice is thought to form first in areas of relatively pure water, such as the xylem (Asahina, 1954), or between the epidermis and mesophyll of leaves (Idle, 1966; Olien et al., 1968). Crystallization advances through the vascular system at an estimated rate of 120 cm min^{-1} at −3 °C and is not affected by the cultivar or growth conditions (Single, 1964). Once the ear has emerged, however, it may then be nucleated by atmospheric ice or infected with ice-nucleating bacteria. Depending on how glaucous the lemma, palea, and awns are, the exposed floral and reproductive tissues may supercool even when exposed to a hoar frost (Single and Marcellos, 1974). Apparently, the waxy surface prevents contact between atmospheric freezing nuclei and internal tissue moisture.

Supercooling provides one mechanism by which frost-sensitive plants or tissues have evolved to avoid freezing damage. Lindlow et al. (1982) suggest that plants do not contain intrinsic ice nuclei active above −8 to −11 °C. Marcellos and Single (1976) demonstrated that dry wheat leaves will supercool to temperatures as low as −14 °C, with the majority of leaves supercooling to −10 °C. Gusta (unpublished observations) determined the degree of supercooling of various plant organs collected from field-grown wheat plants. Leaves supercooled the least, followed by the stem and nodes. The awns, lemma, and palea supercooled 2 to 4 °C more than the leaves.

Only in 6 out of 73 nights could Marcellos and Single (1976) detect stable ice nuclei able to initiate freezing in plants at −5 °C. They concluded that under conditions of a radiation frost neither airborne particles nor ice crystals induced frost formation. In a review on ice nucleation in plants, Lindlow (1983) identified three species of bacteria commonly found as epiphytes on leaf surfaces which are extremely effective ice nucleators at warm subzero temperatures. The most common ice nucleation active (INA) bacteria were *Pseudomonas syringae* Van Hall, followed by *Erwinia herbicola* (Lohnis) Dye and *P. fluorescens* Migula. Many isolates of these bacteria are effective ice nucleators at −2 °C (Lindlow et al., 1978). Wheat plants, growing in controlled environment chambers, have little or no ice nucleating bacteria on their leaves and do not freeze when exposed to temperatures as low as −8 °C for up to 6 h (Gusta, unpublished observations). However, if these plants are sprayed with INA bacteria, freezing occurs within minutes at approximately −3 °C. Under field conditions at Saskatoon, low populations of INA bacteria were found on wheat leaves in the spring in comparison to the higher populations found in late summer, as the plants start to mature in August. Coincident with the increase in INA bacteria is a decrease in supercooling of the plant. From preliminary work it appears that INA bacteria may play a more significant role in causing frost damage in the fall than in the spring.

4–2 WINTER SURVIVAL

4–2.1 Induction and Maintenance of Cold Hardiness

Cold hardening of winter cereals, which is under genetic control, is induced by temperatures < 10 °C (Paulsen, 1968; Svec and Hodges, 1972; Fowler and Gusta, 1977). The energy to drive the metabolic process is obtained either through photosynthesis (Olien, 1967) or from energy reserves in the seed (Andrews, 1960). Cold hardiness is not a static condition, but changes with time, temperature, daylength, maturity, soil moisture, plant moisture, nutrition, and physiological age.

4–2.2 Factors Affecting Winter Survival

Depending upon the location and crop species, reasons for winterkill vary greatly from year to year. The primary causes, as outlined by Salmon

(1933), are heaving, smothering, physiological drought, and freezing of the plant tissues. Ice encasement is a major cause of death in areas of high rainfall (Andrews et al., 1974). Midwinter flooding has also been shown to reduce winter hardiness (Olien, 1967). In the Great Plains of western Canada, the primary cause of winter injury appears to be related to low soil temperatures between November and February. It is essential during this period to have an insulating layer of snow to prevent the soil temperature from going below the critical temperature of the winter cereal. For example, from controlled freeze tests, the crowns of Norstar winter wheat can survive exposure to −23 °C for 12 h without being killed. However, a brief exposure to −24 °C may completely kill the crown tissue.

In areas which experience prolonged periods of subzero temperatures, snow (10–15 cm) is essential for the survival of winter wheat. Snow is required as an insulator to trap residual soil heat and buffer against air temperature extremes. A uniform snow cover is not maintained on open fields due to the effects of wind, even when the snowfall is adequate. Snow dunes are created, which may or may not stabilize, resulting in irregular winterkill. In 1932 in North Dakota, it was demonstrated that seeding winter wheat in standing stubble offered the greatest chance for winter survival (Sarvis and Thysell, 1936). Aase and Siddoway (1979) observed that in Montana under conditions of no snow cover, the soil temperature at crown depth was colder than −16 °C when the air temperatures were below −22 °C. Fields covered with 6 to 7 cm of snow did not go as low as −16 °C even though the air temperature was as low as −35 °C. Fowler (1983) concluded that only 8 to 10 cm of unpacked snow in standing stubble was adequate for the survival of hardy winter wheats in Western Canada. Under these conditions the soil temperature at crown depth would rarely be colder than −11 °C.

In addition to an insulating effect, snow also protects against the dehydration effects of subzero temperatures. Freezing induces severe dehydration of tissue; at −5 °C the water potential is reduced to −60 MPa and at −15 °C it is −185 MPa. The leaves of winter wheat are much more sensitive than the crowns to the desiccating effects of subzero temperatures.

Cold injury increases with the length of exposure to low temperatures (Gusta et al., 1982). Fully cold-hardened winter wheat crowns can tolerate −15 °C for 5 to 6 days, but can only tolerate −18 °C for 24 h and −23 °C for 12 h. Crowns of hardy cultivars could be held at −12 °C for a period of 15 days or longer with little or no damage. Plants held at −3 °C under a snow cover for 5 months lose almost all of their cold hardiness or succumb to the continuous frost.

A summary of the factors affecting winter survival is presented in Fig. 4–1. Although a cultivar may achieve considerable hardiness by early winter, this hardiness may be lost due to various factors. For example, cyclic freezing and thawing results in increased injury from ice crystal

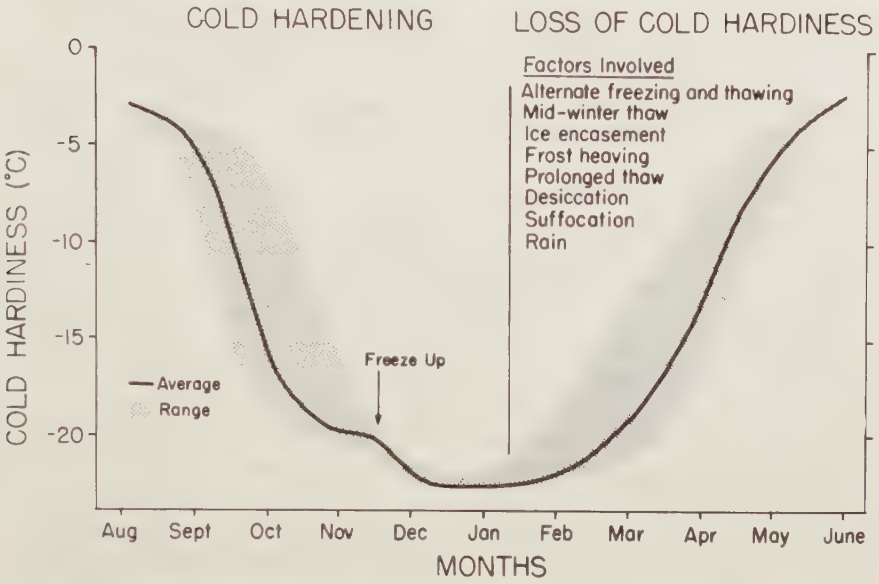

Fig. 4–1. Changes in cold hardiness of 'Norstar' winter wheat under field conditions in Saskatchewan, with primary factors responsible for any loss in cold hardiness.

growth with each freeze (Olien, 1969). Similar effects have been observed by repeated freezing and thawing in controlled freeze tests (Gusta and Fowler, 1977). A midwinter thaw results in flooding of the crown, which increases tissue water content. Gullord et al. (1975) duplicated these conditions in a controlled freeze test and found that the temperature at which flooded crowns were killed was 2 to 7 °C warmer than for nonflooded crowns.

4–2.3 Anatomical Features Associated with Hardiness

Different plant parts of winter cereals possess different levels of cold hardiness. In comparison to the crown and herbage, the roots have only a limited capacity to cold harden. Chen et al. (1983) reported that the roots of Norstar winter wheat and 'Puma' rye cold hardened to only −6 to −7 °C, whereas the crowns cold hardened to −20 and −30 °C, respectively. Gusta (unpublished observation) found that after 4 months storage at −3 to −5 °C, the adventitious roots on hardy cultivars were dead while the crowns were still alive. It is not known whether the roots succumbed to freeze-induced desiccation or to the prolonged period of cold. Several bentgrasses (*Agrostis palustris* Huds.), which are extremely cold hardy (ca. −45 °C), die after prolonged storage at −3 °C, due to desiccation of the roots.

Tillers on the same plant do not possess the same degree of winter survival. Crescini and Tettamanzi (1929) observed that the younger tillers

survived the winter better than the older tillers. Legge et al. (1983) reported that the intermediate to younger tillers were the most cold hardy.

Legge (1979) observed that following a freeze, tillers regenerated from adventitious buds rather than from the intercalary meristem. Although the reason for this is obscure, it may be due to injury of the xylem vessels and the cells of the central and lower region of the crown (Olien, 1961). This region has a high moisture content due to the xylem vessels and the presence of large vacuolated cells. Thus, large ice crystals could form, resulting in mechanical damage to the tissue. This would reduce the vascular connection between the shoots and roots (Pauli, 1960) or result in injury to the tissue which normally gives rise to adventitious roots (Beard and Olien, 1963). Axillary buds may escape injury due to their small undifferentiated cells and their less rigid tissue, compared to the stem region of the parent tiller.

An inverse relationship exists between cold hardiness and the number of tillers, number of leaves, crown root number, and crown root length (Fowler and Gusta, 1977). Crown and leaf water content, plant erectness, crown P content, and total crown sugar content were highly correlated with field survival (Fowler et al., 1981). Leaf water content, combined with plant erectness, was as good an indicator of winter field survival as a controlled freeze test.

It has been suggested that cultivars which have their crowns deep in the soil survive the winter better than cultivars with shallow crowns (Ferguson and Boatwright, 1968; Levitt, 1956). It was theorized that the crown and the coleoptile tiller would be more insulated from temperature extremes. Crown depth is greatly influenced by genotype, depth of seeding, and soil temperature, light, and other environmental factors. However, Fowler and Gusta (1977) found no correlation between crown depth and winter survival of four hardy winter wheat cultivars. Little or no difference in soil temperature could be detected by thermocouples placed next to the crown or next to the coleoptile tiller.

4–2.4 How Plants Freeze

At subzero temperatures, ice first forms in the extracellular spaces where water is the purest. In nature, changes in air temperature are slow (1 to 10 °C h^{-1}) while changes in soil temperature are even slower ($<$ 1 to 5 °C h^{-1}). With such slow cooling rates, water can readily migrate to areas of lower vapor pressure created by the ice. Ice does not grow uniformly through the tissue, but rather at preferred sites, which can accommodate the growing crystal. Ice may first form in the veins (Asahina, 1954) or between the epidermis and mesophyll of leaves (Idle, 1966; Olien et al., 1968). In the crowns, ice may form in the vascular systems where there are large amounts of free water (Olien, 1981). This may disrupt the vascular connections between the upper and lower part of the crown.

Ice is partitioned from the protoplasm by the cell wall and plasma membrane. Since no ice forms inside the protoplast, the cell fluids remain

in a liquid state. Not all of the water in a cell freezes at once due to dissolved cell solutes and its interaction with cellular components. Therefore, the freezing temperature of the osmotically active cell fluid is a sliding function of temperature which can be estimated from the Clapeyron-Clausius equation (Glasstone, 1946).

Prior to freezing, the freezing point depression of cells is generally in the range of -1 to -1.5 °C (0.5–0.7 osmolal). More than 60% of the crown tissue water content is frozen at -4 °C, which results in an increase in cellular fluids to approximately 5 osmolal (Gusta et al., 1975). This increased solute concentration prevents the interior of the cell from freezing. At -10 °C, over 90% of the total freezable water is frozen and the cell has become severely dehydrated (ca. -120 MPa). At -20 °C, nearly all of the freezable water is frozen, except for a small fraction (ca. 0.2–0.5 g of water g^{-1} dry weight) that is held tightly by the cellular compounds and is not available for freezing even at -40 °C. The quantity of water that migrates from the cell to the growing ice crystal is therefore a function of temperature.

During freezing-induced dehydration, the plasma membrane remains attached to the cell wall, causing the cell to collapse (Levitt, 1956; Salcheva and Samygin, 1963; Siminovitch and Scarth, 1938; Johansson, 1970). If the extracellular spaces are too small to accommodate the growing ice crystal, the cells are crushed, ruptured, or separated by splitting of the cell walls along the middle lamella (Levitt, 1956). As the cell wall collapses, the protoplasm is pushed against the outer cell wall in the form of a ring and the plasmatic strands break (Alden and Herman, 1971). Upon thawing, the cell becomes rehydrated and expands back to its original volume. If the cell has been killed by the freeze-thaw cycle, the protoplast may break away from the cell wall and shrink in size. This phenomenon has been termed *pseudo* or *frost plasmolysis* (Siminovitch and Scarth, 1938). If the cells have been injured by freezing, their membranes leak and the cells are unable to regain full turgor.

The reduced semipermeability properties of cell membranes following freeze injury has led many researchers to suggest that membranes are the primary site of injury. Cellular compounds start to leak from the tissue immediately upon thawing, with no measurable lag period. Depending on how homogeneous the tissue is, there is little or no ion leakage prior to exposure to the killing temperature. Results based on microscopic observations (Salcheva and Samygin, 1963), fluorescent changes in cells under frozen conditions (Krasavtsev, 1962), and nuclear magnetic resonance studies (Rajashekar et al., 1980) suggest that freezing injury occurs during the freezing process upon cooling below the frost killing temperature.

4–2.5 Metabolic Changes Associated with Hardening

Siminovitch et al. (1967) demonstrated that cold hardening results in dramatic changes in the cellular constituents, or what they termed

augmentation. Unhardened cells have a large central vacuole and a thin peripheral cytoplasm, whereas cold-hardened cells have a dense cytoplasm with many small vacuoles and a large central nucleus. During hardening there is an increase in the quantity of membranes, particularly the plasma membrane, which has marked invaginations (Pomeroy and Siminovitch, 1971).

Steponkus et al. (1982) studied the freezing behavior of isolated 'Puma' rye protoplasts under a microscope and observed that nonacclimated protoplasts were unable to expand back to their original volume during a freeze-thaw cycle and consequently lysed. These authors attributed lysing to the loss of plasma membrane material during freeze-induced contraction. Upon rehydration the plasma membrane material lost could not be added back fast enough to the plane of the membrane before expansion-induced lysis occurred. In the case of acclimated protoplasts, large surface contractions were reversible and injury was not due to the events that occur during contraction.

Many studies have been conducted on the degree of lipid unsaturation and fluidity of the membranes, since they are the primary site of injury. Marked growth-temperature-dependent alterations in the fatty acid composition and unsaturation of the mitochondrial phospholipids were observed during hardening of four wheat cultivars (Miller et al., 1974). Structural transitions occur at lower temperatures in cold grown material and were quantitatively greater in the winter hardy cultivars. Farkas et al. (1975) also concluded that the degree of lipid unsaturation was correlated with cultivar hardiness. De la Roche et al. (1975) found that the change in lipid unsaturation of the membranes was the same in four wheat cultivars differing in cold hardiness. The increased unsaturation of lipids at hardening temperatures may be more related to vernalization than to cold hardening (de Silva et al., 1975).

It is uncertain whether the reported changes in membrane unsaturation are related to changes in the plasma membrane as they are based on analytical data from crude membrane fractions or total membrane extracts. Uemura and Yoshida (1984) analyzed a plasma membrane enriched fraction from cold hardened winter rye seedlings and found that the degree of fatty acid unsaturation and proportion of phospholipid classes changed only slightly during hardening. These results suggest that fatty acid changes may not be as dramatic as once thought for cold hardening of winter cereals.

A short dehydration period at room temperature will cold harden winter cereals (Cloutier and Siminovitch, 1983). The increased cold hardiness persists even after the plants have been rehydrated. Cell suspension cultures of Norstar winter wheat growing at 21 °C can tolerate −30 °C after 4 days treatment with abscisic acid (Chen and Gusta, 1983). Thus, it appears that the low temperature requirement for hardening can be bypassed in special circumstances.

Within a cereal species a high positive correlation (r=0.9) exists be-

tween crown water content and cold hardiness. However, between species this correlation does not hold. For example, when fully hardened, Norstar winter wheat and Puma rye have the same moisture content, but differ by 10 °C in cold hardiness. The decrease in water content with cold hardening is due to an increase in dry matter accumulation at low temperatures and not to a water deficit.

Cells labelled with radioactive leucine at 21 and 2 °C take up the radio label at nearly the same rate. The rate of turnover of label at 21 °C is several times higher than in cells maintained at 2 °C. These results suggest that for cells to cold harden there must be a slow-down in growth accompanied by an increase in cell metabolites (Robertson, unpublished data).

4–2.6 Breeding for Cold Resistance

The Crimean cultivars introduced from the USSR at the turn of the century have provided the basic germplasm for the production of extremely cold-hardy red winter wheats in the Great Plains of North America (Quisenberry and Reitz, 1974). Almost all of the new strains of hard red winter wheat grown in the Great Plains were developed from hybrids involving the Crimean cultivars. 'Kharkov MC 22', an old MacDonald College selection from USSR wheats, was long regarded as the most cold hardy cultivar, until it was replaced by Norstar in 1977. Two USSR introductions, 'Alabaskaja' and 'Ulianovkia', are significantly more cold hardy than 'Kharkov' and slightly more cold hardy than Norstar. Stushnoff et al. (1983) concluded that the genetic variability for winter hardiness has been largely exhausted. Fowler et al. (1983) have found that the only examples of transgressive segregation for greater winter hardiness were from crosses between parents of moderate or poor hardiness, and selections from these were not as hardy as existing genotypes. In crosses involving extremely hardy parents, transgressive segregation for increased cold hardiness has not been reported (Orlyuk, 1976; Shelepov et al., 1980). This may be due to the fact that all the hardy genotypes identified today are from Crimean stock and possess common genes for cold hardiness. Thomas and Gaudet (1983) suggest that, since all the hardy wheats are derived from Russian accessions, perhaps some gain could be made from Chinese introductions. The Chinese wheat 'E85' has considerable winter hardiness (Everson et al., 1976); it crosses readily with rye and may possess genes for winter hardiness distinct from the Russian selections (Thomas and Gaudet, 1983).

Attempts to transfer the cold hardiness from rye to winter wheat have resulted in the production of triticale that is only about as cold hardy as the wheat parent (Larter, 1973; Dvorak and Fowler, 1978); the cold hardiness of the rye is apparently suppressed in triticale. Grafius (1981) backcrossed wheat to a *Triticum aestivum* × *Agropyron trichophorum* hybrid and selected wheatlike plants whose cold hardiness was similar

to rye. Fedorov (1970) reported that wheat–*Agropyron* amphiploids (2n = 56) were as cold hardy as hardy ryes.

Limin and Fowler (1982) produced a range of amphiploids from interspecific crosses between *T. durum* and *T. aestivum*, *T. dicoccum*, *T. araraticum*, *T. ventricosum*, and *T. tauschii*. None of the amphiploids exceeded the most hardy *T. durum* parent in cold hardiness. The cold hardiness of the parents was not additive in the amphiploid, but apparently was dependent on the specific combining ability of the parents. Limin and Fowler (1983) concluded from crosses of amphiploids with Norstar that there was partial dominance for cold hardiness. Many of the F_2-derived F_3 lines were equal to Norstar in hardiness, suggesting that only a few genes are involved in hardiness.

Brule-Babel (Crop Science Department, University of Saskatchewan, personal communication, 1985), working with reciprocal crosses of very hardy by less hardy wheat parents, could not find any evidence of a cytoplasmic effect on cold hardiness or on the nuclear expression of cold hardiness.

Cell suspension cultures and embryo cultures provide the opportunity to determine whether there is somaclonal variation for cold hardiness within winter wheat. Cell suspension cultures of winter wheat, exposed to cold hardening conditions, will cold harden within a week (Chen and Gusta, 1982; Chen and Gusta, 1983). Abscisic acid at 10^{-5} *M* induces about −30 °C freezing resistance in Norstar cell cultures within 4 days at 21 °C (Chen and Gusta, 1983). Regenerable wheat callus, derived from immature embryo, can also be cold hardened to the same level as the parent plant; it also may be stored at liquid N_2 temperatures if cryoprotectants are added (Chen, unpublished results). Plants can readily be regenerated from these cultures and provide the breeder with a larger number of plants from a single cross. Since wheat cultures can be cold hardened in vitro, studies on the genetics of hardiness from a single cross are possible.

4–3 HIGH TEMPERATURE STRESS

Most crop plants of temperate origin do not tolerate prolonged exposure to temperatures above 35 °C (Christiansen, 1978; Treshow, 1970). Under field conditions, temperatures of 35 to 40 °C are common in many wheat-producing areas of the world. It is very difficult to adequately define heat stress in plants because response depends on thermal adaptation, duration of exposure, and stage of growth (McWilliam, 1980). In the field, duration, temperature, and the rate of temperature change affect thermal adaptation and intensity of high temperature stress. Furthermore, the effects of high temperature are frequently confounded with those of water stress, which usually accompanies high temperature stress (Levitt, 1980a; Threshow, 1970).

The maximum rate of photosynthesis occurs between 20 and 30 °C

for most temperate plants. However, the rate of respiration tends to increase with temperature, to a point where injury to the protoplasm occurs (Larcher et al., 1973). This results from starvation due to excessive usage of photosynthate in respiration. Such chronic effects of high temperature stress usually result in suppressed growth and reduced yield, but rarely cause lethal injury to plants (Christiansen, 1978, McWilliam, 1980). Since there are no visible symptoms of injury, the effect of heat stress on crop plants has largely been ignored in the past.

Many countries experience hot, dry winds during grain filling of wheat. High temperature injury is difficult to estimate in the field, because there is no way to determine what the crop yield would have been in the absence of a high temperature stress (Smika and Shawcroft, 1980). A 17-yr study in Israel showed that grain yield was reduced by 0.76 kg ha^{-1} for each hot, dry day that occurred between flowering and grain filling (Lomas and Shashoua, 1974).

4–3.1 High Temperature Injury of Somatic Tissue

The plant functions most studied in relation to heat stress are protoplasmic streaming (Alexandrov, 1964), respiration (Berry et al., 1975), photosynthesis (Berry, 1975; Bjorkman and Badger, 1979; Pearcy et al., 1977a; Raison and Berry, 1979), membrane permeability (Berry et al., 1975; Martineau et al., 1979), and enzyme inactivation (Levitt, 1980a). Two major structures affected by high temperature are proteins and membranes. Enzyme inactivation at high temperatures is a major cause of growth reduction (Levitt, 1980a), while membrane disruption may alter water, ion, and organic solute movement, photosynthesis, and respiration (Christiansen, 1978).

The photosynthetic apparatus is more sensitive to heat than are respiration, protoplasmic streaming, and ion leakage (Larcher et al., 1973). Photosystem II and photophosphorylation are particularly heat labile in many plants (Bjorkman et al., 1980; Santarius and Muller, 1979). The ultrastructure of thylakoids and a stabilizing effect of soluble nonsugar stroma compounds are involved in the adaptation of the photosynthetic apparatus to high temperatures (Santarius and Muller, 1979).

Feierabend and Mikus (1977) studied growth and development of wheat plants over a temperature range of 22 to 36 °C. Briefly their findings were: the formation of the 70s chloroplast ribosome was inhibited at 34 °C, total amino N remained constant over the temperature range studied, the leaves at 34 °C were 80% of the length at 22 °C, and the leaves were photobleached at 34 °C under continuous light. Total protein content of the high temperature-grown wheat leaves was diminished by 50% as compared to plants grown at 22 °C. Inhibition of chloroplast ribosome synthesis by high temperatures undoubtedly impaired the function of wheat leaves.

In the Pacific Northwest of the USA, poor winter wheat seedling emergence occurs if the crop is sown from August to September, but not

if sown in October (Burleigh et al., 1964). This is probably due to high soil temperature effects in late summer and early fall. The rate of seedling emergence is associated with coleoptile length, and germinating wheat seeds with long coleoptiles generally emerge more rapidly than those with short coleoptiles (Allan et al., 1962). Wheat selections react differently to high temperature in terms of coleoptile length and seedling emergence (Burleigh et al., 1964). Generally, temperatures over 32 °C reduce wheat coleoptile length by inhibiting cell elongation (Allan et al., 1962).

Onwueme and Laude (1972) also reported that there was a reduction in the length of wheat coleoptiles subjected to 46 °C. The stunting effect of high temperatures increased with the duration of the stress and could not be prevented by exogenous applications of indole-3-acetic acid (IAA) or gibberellic acid.

4–3.2 High Temperature Injury of Reproductive Tissue

High temperatures limit field production of several important crops in many regions of the world. Based on fruit-set and yield under high temperature conditions, high temperature tolerant genotypes have been identified in tomato (*Lycopersicon esculentum* Mill.) (Ahmadi and Stevens, 1979; Stevens and Rudich, 1978), bean (*Phaseolus vulgaris* L.) (Halterlein et al., 1980), soybean (*Glycine max* L. Merr.) (Martineau et al., 1979), potato (*Solanum tuberosum* L.) (Mendoza and Estrada, 1979) and sorghum (*Sorghum bicolor* Pers.) (Sullivan and Ross, 1979). The essential steps for successful seed set are: (i) production of viable pollen grains; (ii) transfer of pollen to the stigma; (iii) germination of the pollen grains and growth of the pollen tubes down the style; (iv) union of a male gamete with a viable oocyte; and (v) normal development of the zygote following fertilization. All of these steps are temperature sensitive, but some steps are more heat-labile than the others.

In wheat, exposure to a hot wind for a short period at the boot stage or brief exposure to high temperatures at anthesis can drastically reduce grain number per spike (Smika and Shawcroft, 1980). Grain set is reduced by temperatures higher than 30 °C during the period from the onset of meiosis in the male generative tissue to the completion of anthesis (Smika and Shawcroft, 1980). Saini and Aspinall (1982a) exposed wheat plants to 30 °C under conditions of high relative humidity from the beginning of meiosis in the pollen mother cells to anthesis. Plants exposed to 30 °C for 3 days had 80% of their florets completely male sterile and produced 68% fewer kernels than those grown continuously at 20 °C. The same treatment (30 °C) had no effect when applied at other stages of development.

The reduction in grain set caused by high temperature stress, as described above, was due to both male and female sterility. Pollination of heat-stressed pistils with fertile pollen from unstressed plants resulted in a 21% reduction in grain set (Saini and Aspinall, 1982a). Serial sections through the heat-stressed ovaries just prior to anthesis showed that about

one-third of the ovaries contained abnormal embryo sacs (Saini et al., 1983). Abnormalities ranged from the complete absence of an embryo sac, accompanied by reduced nucleus development, to small embryo sacs that contained the full complement of cells. Following pollination with fertile pollen, heat-stressed and nonstressed stigmas had similar numbers of germinated pollen grains, but fewer pollen tubes reached the ovary in the heat-stressed treatment. Also, some of the ovaries which attracted pollen tubes were not successfully fertilized, probably due to structural abnormalities of the ovaries. The fewer pollen tubes reaching the ovary indicated a reduced capability of the stressed pistils to support pollen tube growth (Saini et al., 1983). The inhibition in pollen growth may be attributable to an effect of the heat stress on pistil development or a lack of attraction from the embryo sac.

The application of abscisic acid (ABA) to developing spikes of wheat, or a water deficit treatment during meiosis in pollen mother cells, causes pollen sterility without affecting female fertility (Saini and Aspinall, 1981). The water stress induced pollen sterility was probably mediated through an increase in endogenous ABA (Morgan, 1980a). In contrast to water stress, high temperature during pollen mother cell meiosis had no effect on the endogenous ABA content of the spikelets (Saini and Aspinall, 1982b). Thus, the responses of wheat plants to water stress and high temperature differ on at least two major accounts. First, high temperature causes both male and female sterility, whereas water stress causes only male sterility. Second, water stress is associated with an increase in endogenous ABA content, but heat stress has no effect on the level of endogenous ABA.

4–3.3 Adaptation to High Temperature

Acclimation to high temperature occurs in microorganisms, plants, and animals (Alexandrov, 1964; Levitt, 1980a). The mechanisms of acclimation are quite complex and combined effects are probably responsible for the general adaptive response (McWilliam, 1980). The mechanisms for adaptation can be at both the morphological level (McWilliam, 1980) and the molecular level (Bjorkman et al., 1980). For example, heat avoidance in *Encelia* involves leaf pubescence, which results in greater reflectance and reduced leaf temperature. Adaptation has been correlated with thermostability and continued activity of proteins and membranes at high temperatures (Levitt, 1980a). Photosynthetic capability and dry matter production are both temperature dependent, displaying similar temperature optima.

Although adaptation to high temperatures has been well characterized in wild plant species, little information is available concerning the adaptation of crop plants to high temperatures in relation to their performance under heat conditions. Knowledge obtained from wild plant species certainly helps to interpret crop responses to high temperature. However, the adaptive mechanism of a wild species may differ from that of the

cultivated species, even if it was originally the same. Such a mechanism may have been altered or obscured during cultural or breeding adaptation (Berry, 1975).

Certain crop plants can acquire heat tolerance by exposure to a gradual increase in temperature. Heat tolerance of a plant at any given time results from its specific hardening and the environmental conditions. The hardening capacity of a plant genotype may vary according to the physiological status, age, and phase of plant development (Larcher et al., 1973). For example, Chen et al. (1982) compared the heat adaptability of heat tolerant and heat susceptible genotypes of bean, potato, soybean, and tomato. They found that all genotypes studied showed increased heat tolerance when subjected to acclimating temperatures of about 35 °C. However, the heat tolerant genotypes heat hardened faster and to a higher level than the susceptible genotypes. For wheat leaves, the ability to heat harden decreased with senescence and maximum hardening of wheat seedlings required an extended period at high temperatures—a regime of 44 °C 6 h/25 °C 16 h, increasing to 54 °C 6 h/25 °C 6 h (cf. Levitt, 1980a).

Above a certain threshold temperature, thermal denaturation and metabolic degradation of proteins occurs. When protein synthesis and/or other adaptive mechanisms can no longer compensate for the high temperature stress, breakdown of cellular functions will occur (Weidner and Ziemens, 1975). Thus, if plants are able to maintain high rates of protein synthesis at high temperatures, they may be able to perform well under a high temperature stress.

Weidner and Ziemens (1975) studied the effects of pretemperature conditioning on the optimum protein synthesis temperature in wheat seedlings. They found that wheat plants grown at 4 °C for 4 days had an optimum rate of protein synthesis at 27.5 °C, whereas plants grown at 36 °C had the highest rate of protein synthesis at 35 °C. The rate of protein synthesis was the same for seedlings pretreated at low, medium, or elevated temperatures, if protein synthesis was measured at 20 °C. The upshifting of the optimum temperature of protein synthesis by high pretreatment temperature indicates that wheat seedlings acclimate to high temperatures.

4–3.4 Heat Shock Proteins

If soybean seedlings are shifted from a growth temperature of 25 to 40 °C there is an inhibition of normal protein synthesis and the synthesis of a new set of proteins known as heat shock proteins (Altschuler and Mascarenhas, 1982). Prolonged exposure to high temperature results in impairment of protein synthesis and death. However, if the seedlings are exposed to 45 °C for 10 min and then transferred to 28 °C, heat shock proteins are synthesized, which provides thermal protection to subsequent exposure to 45 °C (Lin et al., 1984).

Wheat and a number of other plants respond similarly to soybean in that a large number of new proteins of similar molecular weight are

induced by a heat shock treatment (Key et al., 1982). However, a detailed analysis of wheat heat shock proteins has not been reported. According to Key et al. (1982), the major differences among species were the optimum temperature for induction of heat shock proteins, the break-point temperature, the distribution of the 15 to 20 kd heat shock proteins on two-dimensional gels, and the relative level of normal protein synthesis that occurs during heat shock. Although heat shock proteins have been identified in many living organisms ranging from bacteria to human cells, only limited progress has been made in the understanding of the physiological significance of heat adaptation of higher plants.

Altschuler and Mascarenhas (1982) reported that a mild heat shock or a gradual increase in temperature into the heat shock range (40 to 43 °C) enables soybean cells to survive subsequent exposure to a potentially lethal temperature of 52 °C. Thus, a mild stress switches on genes that synthesize new proteins that enable the plant to function at otherwise nonpermissive temperatures (Key et al., 1982). The possible role of heat shock proteins in the adaptation of wheat to high temperature stress is not yet known.

4–4 WATER STRESS

It has been estimated that "about one-third of the world's potentially viable land suffers from an inadequate supply of water, and on most of the remainder, crop yields are periodically reduced by drought" (Kramer, 1980). Most of the world's major wheat growing areas are threatened routinely by drought. Water deficits affect every aspect of wheat growth from seed germination to seed set and final yield. The reader is referred to the reviews by Levitt (1980b), Turner and Kramer (1980), and Mussell and Staples (1979) for detailed information on water stress in plants.

4–4.1 Plant Water Relations

Water potential (ψ) has been widely accepted as a fundamental measure of a plant's water status and as a sensitive indicator of plant water stress. Water potential of the living plant cell is the sum of the component potential arising from the effect of pressure (pressure potential, or ψ_p), solutes (osmotic potential, or ψ_s), and matrix (matrix potential, or ψ_m), and can be expressed as:

$$\psi = \psi_s + \psi_p + \psi_m \qquad [1]$$

Unless the tissue is severely dehydrated (loss of more than 50% water), ψ_m can be ignored since it is negligible in tissues of well-watered plants. Therefore, Eq. [1] can be reduced to:

$$\psi = \psi_s + \psi_p \qquad [2]$$

Pressure potential is usually decreased more than the osmotic potential during the early stages of water stress (Hsiao, 1973). Water potential is generally measured by thermocouple psychrometers or pressure chambers, while osmotic potential is measured on the expressed sap with a psychrometer or an osmometer.

In well-watered wheat plants, the water potential ranges from −0.5 to −1.6 MPa, with slight differences among tissues; the osmotic potential ranges from −1.1 to −1.2 MPa; and the pressure potential ranges from 0.2 to 1.2 MPa (Table 4–1). Under field conditions, leaf water potentials of −2.0 to −3.5 MPa are common. In wheat plants, a water stress markedly reduces water content of the leaves, stems, and (though to a lesser extent) ear structure, but has little or no effect on water content of the grain (Wardlaw, 1971).

4–4.2 Growth, Development, and Yield

Water stress affects the anatomy, morphology, physiology, and biochemistry of plants at every stage of growth (Kramer, 1969). Leaf area, cell size, intercellular volume, and plant size are reduced due to water stress. Cell division and cell expansion are extremely sensitive to a water deficit (Hsiao, 1973). Water stress at certain stages of growth is more injurious than at other stages. In grain crops, the critical period is usually just before reproductive organ formation and right after pollination and fertilization.

Quarrie and Jones (1977) observed the following effects of water stress on development and morphology of wheat plants: a significant reduction in leaf area due to reduced cell division, an increase in size of stomata, a marked increase in the frequency of trichomes on both leaf surfaces, an increase in the total number of cells per unit leaf area, and a reduction in the number of spikelets.

Leaf elongation (Munns and Weir, 1981) as well as apical growth and spikelet formation (Barlow et al., 1977) are inhibited in wheat if the water potential approaches −1.0 MPa. Wardlaw (1971) observed that dry weight accumulation was depressed in both stems and roots by a water stress. Growth of the top internode was much less sensitive to water stress than that of the lower internodes. In addition, tillering was extremely sensitive to a water deficit, resulting in a temporary cessation of tiller development. Keim and Kronstad (1981) reported a 55% reduction in tiller number in water-stressed plants compared to well-watered controls.

Blum et al. (1983) subjected four cultivars of wheat differing in drought resistance to a mild (−0.3 MPa) and severe (−1.0 MPa) water stress using polyethylene glycol (PEG) 6000. Plants exposed to the mild stress had reduced top growth by 22 to 77%, while root growth was 69 to 129% of the controls. Plants subjected to the severe stress had reduced top growth by 66 to 93% and reduced root growth by 66 to 93% as compared to the controls. This demonstrates that water stress always reduces top

Table 4–1. The water status of wheat plants grown in controlled environmental (nonstressed) or field conditions.

Genotype	Growth conditions	Tissue	Water status (MPa)			Reference
			ψ	ψs	ψp	
'Centurk'	Greenhouse	Leaf	−1.6			Allen and Boosalis, 1983
'Heron'	Growth chamber	Apex	−0.9	−1.2	(0.3)†	Pheloung and Barlow, 1981
'Heron'	Growth chamber	Apex	−0.5			Barlow et al., 1977
'Heron'	Growth chamber	Leaf 4	−0.7			Barlow et al., 1977
'Heron'	Growth chamber	Apex	−0.6	−1.2	(0.6)	Munns et al., 1979
'Heron'	Growth chamber	Leaf 7	−0.9	−1.1	(0.2)	Munns et al., 1979
'Heron'	Growth chamber	Leaf 4	−0.9	−1.1	(0.2)	Munns et al., 1979
'Gabo'	Greenhouse	Leaf	−0.5			Saini and Aspinall, 1981
'Gabo'	Greenhouse	Spike	−1.0			Saini and Aspinall, 1981
'Condor'	Greenhouse	Leaf	−1.2		0.1	Morgan, 1980a
'Condor'	Greenhouse	Spike			0.6	Morgan, 1980a
'Chinese Spring' and 'Seeon'	Greenhouse	Leaf	−1.0			Morgan, 1980a
11 genotypes	Field	Leaf	−1.8 to −2.5			Blum et al., 1980
10 genotypes	Field	Leaf	−2.3 to −3.5			Keim and Kronstad, 1981

†Value in parentheses is calculated from water and solute potential according to Eq. [2] on page 129.

growth, but, depending on the severity of the stress and the genotype, root growth may be either reduced or stimulated.

If the leaf water potential falls below −1.2 MPa, wheat grain yield is reduced, especially if the water stress coincides with the period of reduction division in the reproductive organs (Saini and Aspinall, 1981). The effect of water stress on wheat yield is primarily associated with a reduction in the grain number per spike via the induction of male sterility (Morgan, 1980a; Saini and Aspinall, 1981). However, the effect of water stress during the early stage of grain development on final grain yield may be an indirect effect (Wardlaw, 1971). This view is supported by the observation that a significant decline can occur in leaf water potential with little or no change in spike water potential (Morgan, 1980a, Saini and Aspinall, 1981). The induction of male sterility by water stress may be mediated, in whole or in part, through an increase in the endogenous concentration of abscisic acid, which in turn causes inviability of pollen grains (Morgan, 1980b).

Wardlaw (1971) observed that a temporary water deficit during the first 7 days following anthesis significantly reduced final grain weight per ear. Bingham (1966) suggested that the sensitive period to water stress occurs during or a few days before pollen meiosis. However, Saini and Aspinall (1981) subjected wheat plants to a water stress at various stages of floral development and found that the most sensitive stage was after pollen mother cell meiosis. They found that a water deficit during pollen mother cell meiosis resulted in a significant reduction in both the number of grains per spike and percent grain set as compared to well-watered plants. The reduction in grain set was due mainly to infertility in the primary and secondary florets within each spikelet. Water stress reduced grain set in the lower and upper regions of the spike, but not in the middle region. An increase in average grain weight may occur when grain set is reduced by a water stress (Saini and Aspinall, 1981). Total photosynthate supply to the spike limits final grain weight (Wardlaw, 1971).

Hand-pollination of water-stressed plants with pollen from well-watered plants resulted in identical grain sets in both well-watered and water-stressed plants (Saini and Aspinall, 1981). These results confirm that male sterility was the cause of the reduced grain set; female fertility was unaffected. Florets from water stressed plants at the sensitive stage contained shriveled anthers which extruded only partially, and either did not dehisce or dehisced abnormally. Pollen obtained from these abnormal anthers was inviable, shriveled, lacked starch granules, and did not react positively with 2,3,5-triphenyl-2H-tetrazolium chloride ($C_{19}H_{15}CN_4$). Most of the inviable pollen grains ceased to develop soon after release of microspores from the tetrads.

4–4.3 Transpiration

In most plants water stress results in a decrease in transpiration, due to stomatal closure (Hsiao, 1973). Leaf permeability is, in general, well

correlated with size of stomatal aperture and is therefore used as an index of stomatal closure. Transpiration is directly proportional to the vapor-pressure gradient from the leaf to the air, and inversely proportional to the total resistance to water vapor transport of the air boundary layer and of the leaf (Hsiao, 1973). Since stomates control only one part of the total resistance, increased stomatal resistance may not cause a proportional decrease in the transpiration rate.

There is a threshold level of leaf water potential before stomatal closure is affected, however, stomatal closure occurs over a narrow leaf water potential range (0.5 MPa) and results in a 20- to 30-fold increase in leaf resistance (Hsiao, 1973).

Shimshi and Ephrat (1975) reported that wheat cultivars differed widely in their stomatal aperture under adequate moisture conditions. Leaf permeability was significantly correlated with short-term transpiration, short-term photosynthesis, and grain yield. They found that wheat cultivars with a wide stomatal aperture produced higher yields without consuming more water. In contrast, Johnson et al. (1974) reported that the rate of transpiration of wheat leaves and awned spikes decreased linearly with decreasing flag leaf water potential. Flag leaf transpiration and spike transpiration reached zero at -2.8 and -3.1 MPa, respectively. Frank et al. (1973) also found that during the grain-filling stage, stomatal closure on flag leaves of 'Waldron' wheat was completed at -3.1 MPa. Furthermore, the relationship of stomatal closure to leaf water potential depended on both leaf position and leaf age.

Shimshi et al. (1982) compared stomatal response to water stress in *T. aestivum* ('Chinese Spring' and 'Seeon'), *T. longissimum*, and *T. kotschyi*. They found that not all species closed their stomata at the same water potential. In *T. aestivum*, relative leaf permeability decreased at a leaf water potential of -1.1 MPa, whereas the stomata closed in *T. kotschyi* at -2.0 MPa. They also found that the stomata in *T. aestivum* did not start to open until 2 days after rewatering, and even after 5 days the leaf permeability was only 70% of that of nonstressed plants.

4–4.4 Photosynthesis

Water stress severely reduces net photosynthesis in the flag leaf, top internode, and ear of wheat (Wardlaw, 1971). This reduction in CO_2 assimilation may be due to stomatal closure, which restricts the inward diffusion of CO_2 into the leaf. However, there is also evidence of nonstomatal effects on net CO_2 assimilation in leaves subjected to a moderate water stress (Hsiao, 1973).

The relative importance of stomatal and nonstomatal effects on CO_2 fixation is controversial. It appears that impairment of the photosynthetic apparatus occurs at a higher water stress than that which results in stomatal closure (Shimshi et al. 1982). Nonstomatal effects of water stress on photosynthesis include an increase in mesophyll resistance to CO_2 transport, and an increase in the CO_2 compensation point. There is a

reduction in the activity of RuBP carboxylase, and PEP carboxylase, and a reduction in electron transport, photophosphorylation, chlorophyll and protein synthesis (Mayoral et al. 1981).

4–4.5 Respiration

In higher plants a mild water stress may increase, decrease, or have no effect on respiration (Hsiao, 1973). Although respiration frequently increases with a moderate water stress, rates of respiration decline as the stress becomes severe (Gaff, 1980). It was observed in wheat that both dark respiration and photorespiration of wheat leaves are essentially unaffected between −0.4 and −2.0 MPa (Lawlor, 1979).

Pheloung and Barlow (1981) studied respiration in apices, using water-stressed whole plants or isolated apices stressed with a nonpermeating osmoticum. Respiration decreased with decreasing apex water potential, reaching 40% of the nonstress control rate at −5.0 MPa. They concluded that apex respiration was not related to turgor potential. In water-stressed apices, the demand for metabolic energy for respiration decreased with increasing stress, due to reduced growth and protein synthesis. The translocation of carbohydrate to the apex was not affected by the water stress, since the net import to the apex was relatively constant during the first 7 days despite a decrease in the mean water potential from −1.5 to −3.7 MPa. A moderate to severe water stress resulted in a large accumulation of organic solutes (sugars and amino acids). Thus, the major effect of water stress on apex respiration was related to the cessation of growth, which was not limited by the supply of respiratory substrates.

Gordon et al. (1975) studied the effect of dehydration on the respiration of wheat roots. A 35 to 40% water loss by the roots resulted in: (i) respiration decreased to 40% of the nonstressed control; (ii) electron transport on the NADH cytochrome b sector was reduced, as judged by a decrease in sensitivity to 1,2,12,12a-tetrahydro-8,9 dimethoxy-2-(1-methylethenyl)-[1]benzopyrano[3,4-b]furo[2,3-h][1]-benzopyrano-6(6H)-one (rotenone, $C_{23}H_{22}O_6$); (iii) loss of inhibition of the electron transport system by $C_{26}H_{36}N_2O_9$ (antimycin) and HCN (hydrogen cyanide); and (iv) swelling of mitochondrial cristae and endoplasmic reticulum cisterns. Similar observations have also been made in other plants (Hsiao, 1973).

4–4.6 Protein Synthesis

Protein synthesis in rapidly growing tissue is extremely sensitive to water stress (Hsiao, 1973). For example, in *Avena* coleoptiles water stress reduced the rate and changed the pattern of protein synthesis (Dhindsa and Cleland, 1975). Mayoral et al. (1981) found that the concentration of total soluble protein, expressed per gram dry weight, in leaves of *T. aestivum* and *T. longissimum* decreased when the leaf water potential decreased from the unstressed value of −0.8 MPa. However, in *T. kotschyi* leaves, the concentration of total soluble protein did not change

until the water potential decreased to −2.1 MPa. A decrease in protein content in response to water stress may be due in part to an increase in degradation (Hsiao, 1973).

Barlow et al. (1977) found that the polyribosomal content of unstressed apices was about 50% of the total ribosome population and remained at about 50% as the apex grew in size over the experimental period. The polyribosome content was reduced by 50% when the water potential of the apex was reduced below −1.2 MPa. However, the total number of ribosomes extracted from stressed and control apices was similar, indicating that the ribosomes were not degraded. Hsiao (1973) reported that decreases in polyribosomes in stressed maize leaves occured after growth was reduced and are, therefore, likely to be a result of the growth inhibition rather than the cause.

4–4.7 Hormonal Changes

Most plant species undergo dramatic and rapid change in their endogenous hormone levels when subjected to water deficit stress (Walton, 1980). The reduction in cellular turgor which accompanies water stress may be the major factor responsible for triggering changes in the hormonal balance of the plant (Wright, 1978). There is increasing evidence that when plants are water stressed, water loss can be reduced by mechanisms such as: (i) partial or complete stomatal closure; (ii) increase in hydraulic conductivity of root membranes (Powell, 1978); (iii) osmotic adjustment (Turner and Jones, 1980); and (iv) the increased growth of roots (Caldwell, 1976). Plant hormones have been implicated as factors in controlling or coordinating many of these mechanisms.

4–4.7.1 Abscisic Acid and Ethylene

In wheat plants, the changes in ABA and ethylene in relation to water deficit have been studied relatively extensively. There is inadequate information to draw any conclusions about the roles of other phytochromones (auxin, gibberellic acid, and cytokinin) in wheat water stress, and the following discussion is therefore limited to ABA.

Absisic acid was found to increase dramatically in wilted, excised wheat leaves (Wright, 1969), and in leaves of water-stressed wheat plants (Wright and Hiron, 1969). Absisic acid accumulation was dependent on the length of the wilting period, the temperature, and the degree of leaf water deficit. The ABA content of nonstressed, etiolated and green leaves were 28 and 44 mg kg^{-1} fresh weight, respectively. When leaves were exposed to a stream of air for 20 min to give a 9% water loss and then incubated for 4 h, the ABA contents were 294 and 257 mg kg^{-1} fresh weight for etiolated and green leaves, respectively.

Osmotic stress, induced by osmotically active agents such as NaCl, mannitol, and PEG, also induce ABA accumulation. In wheat plants (Wright, 1978), a PEG-induced root stress resulted in wilting of the shoots

and a final water deficit of 9%. The leaf ABA level increased from 23 to 171 mg kg^{-1} fresh weight within 4 h.

In water-stressed wheat leaves, a sigmoid relationship exists between ABA levels and decreasing leaf water potential (Wright, 1977). Because of the sigmoidal nature of the curve, there was no distinct threshold water potential value triggering ABA accumulation. Wright (1978) proposed that ABA may begin to accumulate in plants if the leaf water potential is 0.2 MPa below the normal daytime potential.

The critical value of leaf water potential that triggers ABA accumulation corresponded to a zero or near zero turgor potential (Davis and Mansfield, 1983). From these results, it is assumed that turgor, rather than total water potential, is the controlling component for triggering ABA accumulation. If this is true, then changing to a more negative cellular osmotic potential (as in the case of osmotic adjustment) would lower the critical water potential for ABA accumulation.

The increase in ABA levels in response to water stress is due to de novo synthesis rather than release of bound ABA (Wright, 1978). Milborrow and Noddle (1970) fed turgid wheat leaves with racemic [2-^{14}C]-diols of ABA and observed that the diols were rapidly oxidized to ABA during wilting. According to Milborrow (1974), there are three mechanisms operating the stress-ABA response: (i) a rapid synthesis of ABA triggered by wilting; (ii) a stop message when sufficient ABA has been formed; and (iii) destruction or cessation of ABA synthesis when turgor is regained.

The biosynthesis of ABA in leaves is generally confined to chloroplasts (or leucoplasts), although other sites of synthesis are also possible (Walton, 1980). Mansfield et al. (1978) proposed that farnesol, a sesquiterpernoid closely related to ABA, causes the release of stored ABA from chloroplasts into the cytosol. This is based on the observation that an increase in farnesol content occurs in sorghum during the early stages of water stress and application of exogenous farnesol to whole leaves of sorghum brought about a reversible suppression of transpiration (Ogunkanmi et al., 1974). Application of 2×10^{-3} *M* farnesol to turgid leaves of spinach (*Spinacia oleracea* L.) induced the formation of almost as much ABA as a wilting treatment (Milborrow, 1979).

The functions of ABA in response to water stress (Davis and Mansfield, 1983; Walton, 1980) include: (i) reduced transpirational water loss by closure of stomata and inhibition of stomatal opening; (ii) increased flux of water into the roots; (iii) inhibition of shoot/root growth; and (iv) rapid accumulation of proline and betaine.

Exogenous ABA applications reduced stomatal conductance in leaves of a droopy potato mutant (Quarrie, 1982) and a flacca tomato mutant (Tal et al. 1974). In excised wheat and barley leaves, exogenous ABA applications resulted in rapid stomatal closure (Mizrahi et al., 1974). Their work also showed that the survival of water stressed barley and wheat leaves was prolonged by the application of ABA.

Quarrie and Jones (1977) compared the effects of ABA and water stress on both the leaf morphology and floral development in spring wheat. They found that both water stress and exogenous ABA resulted in wheat plants with smaller leaves and fewer spikelets per ear. Both ABA treatment and water stress decreased mean cell size, reduced the number of stomata per leaf and increased production of trichomes. From these results they concluded that ABA could mediate many of the responses observed in wheat plants subjected to a prolonged water stress.

Kirkham (1983) studied the effects of exogenous ABA applications to leaves of a drought sensitive ('Ponca') and a drought resistant ('Kanking') winter wheat. In well-watered plants, ABA closed the stomata of both cultivars, and the stomatal resistance of water-stressed and ABA-treated plants was less than in non-ABA-treated but weather stressed plants. Absisic acid decreased the water potential and osmotic potential of Ponca, but had no effect on nonstressed Kanking. However, under water stress conditions, ABA increased the water and osmotic potentials of Ponca, but had no effect on Kanking. The overall effect of ABA was to make the drought sensitive genotype behave as a drought resistant genotype under water stress conditions.

As mentioned earlier, water stress reduces the number of seeds set per spikelet, through an increase in male sterility. Morgan (1980b) explored the possible role of ABA in reducing grain set in water-stressed wheat plants. Wheat plants under water stress showed no change in seed set until the leaves had zero turgor. The reduction in seed set was not related to either spikelet turgor or spikelet water content. During water stress, ABA contents in turgor and wilted leaves were 23.5 and 143.0 ng g^{-1} fresh weight, respectively, whereas in the spikelet, ABA increased from 35.2 to 111.0 ng g^{-1} fresh weight. The reduction in seed set in the absence of water deficits in the spikelets suggests that the ABA effect is indirect. This is further supported by the result that exogenous application of ABA at 10 and 30 mg L^{-1} at meiosis reduced seed set by 43 and 27% as compared to the controls. The reduction in seed set due to ABA application at meiosis was associated with distorted pollen grains devoid of starch granules. These pollen grains were identical to those obtained from water-stressed plants.

Quarrie (1980) reported significant cultivar differences in water potential and ABA concentration when eight wheat cultivars were subjected to drought. Changes in the water deficit accounted for 73 to 98% of the variation in ABA concentration in the different cultivars. Since conductance shows little further response to endogenous ABA concentration in excess of -0.8 MPa, a higher concentration of ABA would not be expected to increase grain yield per unit of water consumed. Genetic differences in the ability to accumulate ABA in response to water stress in wheat are heritable (Quarrie, 1981). The absence of a large maternal influence on the level of ABA accumulation in wheat implies that plastid genes are not critical in determining differential ABA accumulation. In

maize, high ABA contents in the F_1 generation were found only when the high ABA line was used as the female parent (Larque-Saavedra and Rodriguez, 1979).

In a reciprocal cross between 'Chinese Spring' (a low ABA genotype) and 'TW 269/9' (a high ABA genotype), Quarrie and Henson (1982) found that the ABA level of the F_1 population was midway between the two parents. These results suggest that ABA is not under maternal control and that plastid genes are not involved. However, there is a maternal influence in maize (Larque-Saavedra and Rodriguez, 1979).

Ethylene acts as a plant hormone and is involved in growth, development, ripening, abscission, and senescence (Abeles, 1973). Increased ethylene production occurs in response to drought, mechanical wounding, and radiation stresses (cf. Apelbaum and Yang, 1981). This hormone may be involved in the ability of the plant to cope with stress. For example, an increase in ethylene in droughted cotton plants resulted in leaf abscission, which in turn reduced water loss (McMichael et al., 1972).

A burst in ethylene occurred within 4 to 6 h in wheat leaves subjected to water stress (Wright, 1977; Apelbaum and Yang, 1981). The quantity of ethylene produced was related to the severity of water deficit of the leaf tissue. A sigmoid relationship exists between the increase in ethylene formation and decreasing leaf water potentials. Apelbaum and Yang (1981) found that if there was a 2% water loss in wheat leaves, ethylene production increased, reached a maximum at 9% water loss, and then decreased with a further water loss.

Foliar applications of BA(6-benzyladenine) stimulated ethylene formation, whereas ABA counteracted this effect and also inhibited ethylene synthesis induced by water stress (Wright, 1980). Indoleacetic acid and GA_3 also stimulated ethylene synthesis under water-stress conditions. From these results, Wright (1980) speculated that the hormonal balance at the onset of water stress determines the amount of ethylene produced.

The conversion of S-adenosyl methionine (SAM) to 1-aminocylopropane-1-carboxylic acid (ACC) is a key reaction in water deficit-induced ethylene production (Apelbaum and Yang, 1981). Absisic acid inhibits the accumulation of ACC, resulting in the inhibition of ethylene production, whereas BA and IAA increased endogenous ACC and stimulated ethylene production (McKeon et al., 1982).

4–4.8 Osmotic Adjustment

Osmotic adjustment, in higher plants, refers to "the lowering of osmotic potential arising from the net accumulation of solutes in response to water deficits or salinity" (Turner and Jones, 1980). The degree of adjustment varies with species, cultivars, and different organs of the same plant (Morgan, 1980a). Osmotic adjustment occurs in the leaves, hypocotyls, roots, apices, and reproductive organs of several plant species (cf. Morgan, 1980a). The degree of osmotic adjustment is influenced by factors such as the rate of development of the water deficit, the degree of

water deficit, genotypes, and environmental conditions such as temperature and light (Turner and Jones, 1980).

Mechanisms such as stomatal closure, or a reduction in leaf area, are effective in reducing water loss, but result in a loss in productivity and yield. Osmotic adjustment, on the other hand, provides the potential for maintaining photosynthesis and growth, at least in some parts of the plant, as the water deficit increases (Turner and Jones, 1980).

Young wheat leaves and enclosed shoot apices were able to osmotically adjust, whereas fully expanded leaves did not (Munns et al., 1979). Sugars were the main solutes that contributed to osmotic adjustments and the increase was greater in young, unemerged leaves than in fully expanded leaves (Munns and Weir, 1981). Proline, amino acids, malate, and K did not contribute substantially to osmoregulation. The apex of wheat plants can withstand a water potential of −6.0 MPa and still recover when rewatered, whereas fully expanded leaves die at water potentials lower than −3.3 MPa (Barlow et al., 1977).

Wheat genotypes can, according to Morgan (1977), be divided into two categories in regard to osmoregulation. In the first category, there is a linear decline in turgor potential until the water potential equals the osmotic potential. In the second category, the osmotic potential declines at the same rate as the water potential, maintaining a positive turgor. Thus, if relative water content were plotted against osmotic potential, there would be two distinct linear phases. In the first phase (osmotic potential from −1.5 to −3.0 MPa), there is virtually no change in relative water content and the decline in osmotic potential is similar to that observed in plants which did not osmoregulate. Blum et al. (1983) found a positive correlation between yield and osmoregulation.

4–4.9 Morphological Adaptation

One general response of plants to water stress is a marked reduction in leaf area. In the stressed plants, leaf area reduction is the result of reduced growth and of the senescence of older leaves. Leaf growth is restricted in stressed plants due to the sensitivity of cell division and expansion to water deficits (Hsiao, 1973). Water stress also reduces leaf area by enhancing senescence of the physiologically older leaves and through its effect on leaf shedding. An important advantage of reduction in leaf area in response to water deficit is the associated reduction in water loss, delaying the onset of more severe stress (Gaff, 1980). However, a reduction in leaf area will also reduce CO_2 assimilation and result in a reduced yield.

In wheat, the leaf area is fixed at the flowering stage. Under dryland conditions wheat yield is inversely related to the rate of leaf senescence after flowering, and leaf senescence is related to plant water stress (Begg, 1980). On the other hand, the senescence of older leaves could substantially reduce the rate of transpiration without much effect on yield because

older leaves supply relatively little photosynthate to the developing grain in comparison to the flag leaf (Begg, 1980).

Once leaf area development is complete, one of the main mechanisms for adapting to stress is through changes in leaf angle. This includes passive wilting response, active leaf movements, and leaf rolling (Gaff, 1980). In grasses, leaf rolling is a common response to stress and results in a 50 to 70% reduction in transpiration, through both a marked reduction in effective leaf area and a more vertical leaf orientation.

A disadvantage of the morphological adaptations that occur during growth and development of crops is that they are largely irreversible. This is particularly true in determinate crops, since they have no scope for compensation through an increase in leaf number. Thus, the growth or yield potential that has been lost cannot be fully recovered upon return to a more favorable water supply.

4–4.10 Proline Accumulation

Total free amino acids increase in water-stressed leaves, with proline being the most pronounced (Hsiao, 1973; Levitt, 1980b). The accumulation of free proline in water-stressed leaves has been observed in many plant species (Stewart and Hanson, 1980), including wheat (Tan and Halloran, 1982). The metabolic changes that cause proline to accumulate, and the possible association with drought resistance of plants, have been extensively reviewed by Stewart and Hanson (1980).

The observed proline accumulation in water-stressed plants is due to: (i) stimulated synthesis due to loss of feedback inhibition; (ii) inhibited oxidation, probably due to effects on mitochondria; and (iii) impaired protein synthesis (Stewart and Hanson, 1980). Proline accumulation is likely determined by a combination of all three changes, and also by the rate of proline export via the phloem (Stewart and Hanson, 1980).

Stewart and Hanson (1980) conclude that, although proline accumulates to extremely high levels in response to water stress, its contribution to plant adaptation to water stress is probably not significant.

4–4.11 Selection and Breeding for Drought Resistance

The reaction of plants to water stress is important from two standpoints, survival and productivity. While survival is important for native vegetation, productivity or grain yield is the major concern for most crop plants (Begg, 1980). Thus, tolerance to a moderate water stress is of significance to crop plants, whereas plants which can survive a severe water stress would be expected to have low productivity (Kramer, 1980).

Water stress affects almost all aspects of plant function (Hsiao, 1983; Kramer, 1969, 1980; Levitt, 1980b), and nearly all biochemical and physiological processes in plants are relevant components of yield (Townley-Smith and Hurd, 1979). Since photosynthesis is the major substrate source for yield, all genes that affect photosynthesis also affect yield. Thus, the

capability of plants to photosynthesize during and following a water stress is an important index of drought resistance (Lawlor, 1979). Physiological parameters such as relative growth rate, net assimilation rate, leaf area, leaf angle, net CO_2 exchange rate, stomatal number, stomatal resistance, photorespiration, etc., all have the potential to affect yield. From an agronomical point of view, possible approaches to improving wheat drought resistance include selection for: early maturity, rapid growth, an extensive root system, and osmotic adjustment (Stewart and Hanson, 1980; Quisenberry, 1982). Early maturity is important if the drought occurs late in the growing season. Kramer (1980) estimated that, in Kansas and Nebraska, wheat genotypes that mature earlier than the cv. Kharkof yield about 60 kg ha^{-1} greater.

Theoretically, any morphological or physiological improvement that reduces transpiration or increases absorption should postpone the water deficit and reduce the harmful effect of water stress. In wheat, rapid growth, an extensive root system, and osmotic adjustment have been used as criteria in selecting for drought resistant genotypes.

The ability of a plant to absorb water is dependent on the extent and pattern of root development. The majority of wheat roots are distributed in the 0- to 60-cm layer. A deep root system, which enables the plant to utilize moisture below 60 cm, has been used in breeding for drought avoidance (Townley-Smith and Hurd, 1979). Wheat often must rely on stored water in the soil, and it is an advantage to have roots with a small vessel diameter and high hydraulic resistance (Passioura, 1972; Richards and Passioura, 1981). This enables the plants to conserve water during early growth and thus have more water available during the grain-filling period.

To select wheat genotypes for drought resistance, a simple, rapid, nondestructive screening method is required. Numerous techniques have been proposed, but no single test has sufficient reliability to determine overall cultivar drought response (Nass and Sterling, 1981).

4–5 FUTURE RESEARCH NEEDS

Research and management practices aimed at overcoming environmental stress limitations to increased yield have demonstrated that significant progress can be made. Crop losses have been reduced and production has been extended into climatic areas which were considered marginal by previous standards. An example of this is the successful production of winter wheat on the northern edge of the Great Plains by seeding into standing stubble which acts as a snow trap. This is an example where the environmental stress has been partially alleviated, allowing stability of production. In areas of limited rainfall, seeding of spring wheat into standing stubble or on fields with snow trap strips has resulted in a yield advantage when compared to tilled fields. These stubble and snow trap strips result in a more uniform distribution of snow over

the fields and in the spring, the snow melt intake efficiency is increased. The standing stubble also reduced evaporative losses due to heat and wind.

Boyer (1982) concluded that the genetic potential for high productivity is already present in crops, but productivity is limited due to abiotic stresses. In breeding programs, genotypes often are selected under conditions of high fertility and adequate moisture. Boyer (1982) has suggested that selections should be made under conditions more likely to be encountered in the field rather than under ideal conditions.

Plant breeders have relied heavily on selection for yield and understandably could not wait for the fundamental research of the physiologists and molecular biologists. However, in many cases yield has reached a plateau with only small gains being made. Therefore, there is now a greater need for interaction between the breeder and fundmentalists to obtain the information on adaptive responses and heritability. Simple, nondestructive, and rapid techniques to screen large numbers of segregating populations are lacking. Such tests may never be developed for all stresses. Nevertheless, significant advances have been made in selection techniques, even though they may still be rather coarse screens.

Genetic engineering may have certain advantages in selecting for superior genotypes and in understanding the adaptive responses. Selecting somaclonal variants under stress conditions has the advantage that the whole genome is not disrupted, as is done in wide crosses, using wild species as a source of new genes. Often crosses between species do not produce the expected results. For example, the hardiness of winter rye is not expressed in triticale. However, if the genes responsible for the adaptation response can be identified and cloned, they may then be introduced into economic crops to obtain superior genotypes.

Future research on stress physiology should be exciting. Techniques are being developed by genetic engineers to manipulate genes to produce superior genotypes. Research of this nature allows a much wider horizon than was possible in the past.

REFERENCES

Aase, J.K., and F.H. Siddoway. 1979. Crown-depth temperatures and winter protection for winter wheat survival. Soil Sci. Soc. Am. J. 43:1229–1233.

Abeles, F.B. 1973. Ethylene in plant biology. Academic Press, New York.

Ahmadi Al, A.B., and M.A. Stevens. 1979. Reproductive responses of heat-tolerant tomatoes to high temperatures. J. Am. Soc. Hortic. Sci. 104(5):686–691.

Alden, J., and R.K. Hermann. 1971. Aspects of the cold hardiness mechanism in plants. Bot. Rev. 37:37–142.

Alexandrov. V.Y. 1964. Cytophysiological and cytoecological investigations of heat resistance of plant cells toward the action of high temperatures. Q. Rev. Biol. 39:35–77.

Allan, R.E., O.A. Vogel, and J.R. Burleigh. 1962. Length and estimated number of coleoptile parenchyma cells of six wheat selections grown at two temperatures. Crop Sci. 2:522–524.

Allen, M.F., and M.G. Boosalis. 1983. Effects of two species of Vamycorrhizal fungi on drought tolerance of winter wheat. New Phytol. 93:67–76.

Altschuler, M., and J.P. Mascarenhas. 1982. The synthesis of heat shock and normal proteins at high temperatures in plants and their possible roles in survival under heat stress. p. 321–327. *In* M.J. Schlesinger et al. (ed). Heat shock: From bacteria to man. Cold Spring Harbor, NY.

Andrews, J.E. 1960. Cold hardiness of sprouting wheat as affected by duration of hardening and hardening temperature. Can. J. Plant Sci. 40:94–103.

Andrews, C.J., M.K. Pomeroy, and I.A. de la Roche. 1974. Changes in cold hardiness of overwintering winter wheat. Can. J. Plant Sci. 54:9–15.

Apelbaum, A., and S.F. Yang. 1981. Biosynthesis of stress ethylene induced by water deficit. Plant Physiol. 68:594–596.

Asahina, E. 1954. A process of injury induced by the formation of spring frost on potato sprout. Low Temp. Sci. Ser. Bull. 13–24.

Barlow, E.W.R., R. Munns, N.S. Scott, and A.H. Reisner. 1977. Water potential, growth and polyribosome content of the stressed wheat apex. J. Exp. Bot. 28:909–916.

Beard, J.D., and C.R. Olien. 1963. Low temperature injury in the lower portion of *Poa annua* L. crowns. Crop Sci. 3:362–363.

Begg, J.E. 1980. Morphological adaptation of leaves to water stress. p. 33–42. *In* N.E. Turner and P.J. Kramer (ed.) Adaptation of Plants to Water and High Temperature Stress. John Wiley and Sons, New York.

Berry, J.A. 1975. Adaptation of photosynthetic process to stress. Science 188:644–650.

----, D.C. Fork, and S. Garrison. 1975. Mechanistic studies of thermal damage to leaves. Year Book—Carnegie Inst. Washington 74:751–759.

Bingham, J. 1966. Varietal response in wheat to water supply in the field and male sterility caused by a period of drought in a glasshouse experiment. Ann. Appl. Biol. 57:365–377.

Bjorkman, O., and M.R. Badger. 1979. Time course of thermal acclimation of the photosynthesis apparatus in *Neruim oleander*. Year Book—Carnegie Inst. Washington 74:748–751.

----, ----, and P.A. Armand. 1980. Response and adaptation of photosynthesis to high temperatures. p. 233–249. *In* N.C. Turner and R.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Blum, A., J. Mayer, and G. Gozland. 1983. Association between plant production and the some physiological components of drought resistance in wheat. Plant Cell Environ. 6:219–225.

----, B. Sinmena, and O. Ziv. 1980. An evaluation of seed and seedling drought tolerance screening tests in wheat. Euphytica 29:727–736.

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443–448.

Burleigh, J.R., R.E. Allan, and O.A. Vogel. 1964. Effect of temperature on coleoptile elongation in eight wheat varieties and selection. Agron. J. 56:523–524.

Caldwell, M.M. 1976. Root extension and water absorption. p. 63–85. *In* Lange et al. (ed.) Water and Plant Life. Ecological Studies, Vol. 19. Springer-Verlag New York, New York.

Chen, P.M., and L.V. Gusta. 1982. Cold acclimation of wheat and smooth brome-grass cell suspensions. Can. J. Bot. 60(7):1207–1211.

Chen, T.H-H., Z.Y. Chen, and P.H. Li. 1982. Adaptability of crop plants to high temperature stress. Crop Sci. 22:719–725.

----, and L.V. Gusta. 1983. Abscisic acid-induced freezing resistance in cultured plant cells. Plant Physiol. 73:71–75.

----, ----, and D.B. Fowler. 1983. Freezing injury and root development in winter cereals. Plant Physiol. 73:773–777.

Christiansen, M.N. 1978. The physiology of plant tolerance to temperature extremes. p. 173–191. *In* G.A. June (ed.) Crop tolerance to suboptimal land conditions. American

Society of Agronomy, Crop Science Society of America and Soil Science Society of America, Madison, WI.

Cloutier, Y., and D. Siminovitch. 1983. L'induction de la resistance au froid par la secheresse: Une method rapid et economique pour teste et selectionner des cultivars resistants de cereales d'hiver. Can. J. Plant Sci. 63:573–580.

Crescini, F., and A. Tettamanzi. 1929. Sulla resistenza del grano alli basse temperature. Ital. Agric. 66:546–552.

Davis, W.J., and T.A. Mansfield. 1983. The role of abscisic acid in drought avoidance. p. 237–268. *In* F.T. Addicott (ed.) Abscisic Acid. Praeger, New York.

de la Roche, I.A., M.K. Pomeroy, and C.J. Andrews. 1975. Changes in fatty acid composition in wheat cultivars of contrasting hardiness. Cryobiology 12:506–512.

de Silva, N.S., P. Weinberger, M. Kates, and I.A. de la Roche. 1975. Comparative changes in hardiness and lipid composition in two near-isogenic lines of wheat (spring and winter) grown at 2 °C and 24 °C. Can. J. Bot. 53:1899–1905.

Dhindsa, R.S., and R.E. Cleland. 1975. Water stress and protein synthesis II. Interaction between water stress, hydrostatic pressure and abscisic acid on the pattern of protein synthesis in *Avena* coleoptiles. Plant Physiol. 55:782–785.

Dvorak, J., and D.B. Fowler. 1978. Cold hardiness potential for triticale and tetraploid rye. Crop Sci. 18:477:478.

Everson, E.H., C.R. Olien, R. Peare, W.D. Worral, and J.A. Webster. 1976. Winterhardiness. Wheat Annu. Newsl. 22:89–90.

Farkas, T., D.E. Deri-Hadlaczky, and A. Belea. 1975. Effects of temperature upon linolenic acid level in wheat and rye seedlings. Lipids 10:331–334.

Federov, A.K. 1970. The frost resistance of wheat-*Agropyron* hybrids. Dokl. Akad. Nauk. SSSR 14(3):705–707.

Feierabend, J., and M. Mikus. 1977. Occurrence of a high temperature sensitivity of chloroplast ribosome formation in several higher plants. Plant Physiol. 59:863–867.

Ferguson, H., and G.O. Boatwright. 1968. Effects of environmental factors on the development of the lower node and adventitious roots of winter wheat (*Triticum aestivum*). Agron. J. 60:258–260.

Fowler, D.B. 1983. The effect of management practices on winter survival and yield of winter wheat produced in regions with harsh winter climates. p. 238–282. *In* D.B. Fowler et. al. (ed.) New frontiers in winter wheat production. Division of Extension and Community Relations, University of Saskatchewan, Saskatoon.

----, and L.V. Gusta. 1977. Influence of fall growth and development on cold hardiness of rye and wheat. Can. J. Plant Sci. 57:751–755.

----, ----, and N.J. Tyler. 1981. Selection for winterhardiness in wheat. III. Screening methods. Crop Sci. 21:896–901.

----, A.E. Limin, and L.V. Gusta. 1983. Breeding for winter hardiness in wheat. p. 136–184. *In* D.B. Fowler et al. (ed.) New frontiers in winter wheat production. Division of Extension and Community Relations, University of Saskatchewan, Saskatoon.

Fox, P.N., and A.A. Rosielle. 1982. Reference sets of genotypes and selection for yield in unpredictable environments. Crop Sci. 22:1171–1174.

Frank, A.B., J.F. Power, and W.O. Willis. 1973. Effect of temperature and plant water stress on photosynthesis, diffusion resistance, and leaf water potential in spring wheat. Agron. J. 65:777–780.

Gaff, D.F. 1980. Protoplasmic tolerance of extreme water stress. p. 207–230. *In* N.C. Turner and P.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Glasstone, S. 1946. Textbook of physical chemistry. 2nd ed. D. Van Nostrand Reinhold Co., New York.

Gordon, L.K., V.Y. Alekseeva, A.A. Bichurina, A.I. Golubev, L.A. Kasshapova, O.O. Chernysh, and N.N. Gerasimov. 1975. Changes of respiratory metabolism and cell ultrastructure in roots of wheat during dehydration. Soviet Plant Physiol. (Engl. Transl.) 22:804–808.

Grafius, J.E. 1981. Breeding for winterhardiness. p. 161–174. *In* C.R. Olien and M.N. Smith (ed.) Analysis and improvement of plant cold hardiness. CRC Press, Boca Raton, FL.

Gullord, M., C.R. Olien, and E.H. Everson. 1975. Evaluation of freezing hardiness in winter wheat. Crop Sci. 15:153–157.

Gusta, L.V., M.J. Burke, and A.C. Kapoor. 1975. Determination of unfrozen water in winter cereals at subfreezing temperatures. Plant Physiol. 56:707–709.

----, and D.B. Fowler. 1976. Dehardening and rehardening of spring-collected winter wheats and a winter rye. Can. J. Plant Sci. 56:755–779.

----, and ----. 1977. Factors affecting the cold survival of winter cereals. Can. J. Plant Sci. 57:213–219.

----, ----, and N.J. Tyler. 1982. Factors influencing hardening and survival in winter wheat. p. 23–40. *In* P.H. Li and A. Sakai (ed.) Plant cold hardiness and freezing stress mechanisms and crop implications. Vol. II. Academic Press, New York.

Halterlein, A.J., C.D. Clayberg, and D. Teare. 1980. Influence of high temperature on pollen grain viability and pollen tube growth in anatomy in wheat (*Triticum aestivum* L.) Aust. J. Plant Physiol. 10:137–144.

Harrington, J.B. 1936. The reaction of wheat hybrids to a spring frost. Can. J. Res. 14:185–189.

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519–570.

Idle, D.B. 1966. The photography of ice formation in plant tissues. Ann. Bot. (London) 30:199–209.

Johansson, N.O. 1970. Ice formation and frost hardiness in some agriculture plants. Natl. Swed. Inst. Plant Prot. Contrib. 14(132):364–382.

Johnson, R.R., N.M. Frey, and D.N. Moss. 1974. Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. Crop Sci. 14:728–731.

Keim, D.L., and W.E. Kronstad. 1981. Drought response of winter wheat cultivars grown under field stress conditions. Crop Sci. 21:11–15.

Key, J.L., C.Y. Lin, E. Ceglarz, and F. Schoffl. 1982. The heat shock response in plants: Physiological considerations. p. 329–336. *In* M.J. Schlesinger et al. (ed.) Heat Shock: From Bacteria to Man. Cold Spring Harbor, NY.

Kirkham, M.B. 1983. Effect of ABA on the water relations of winter wheat cultivars varying in drought resistance. Physiol. Plant 59:153–157.

Kramer, P.J. 1969. Plant and soil water relationships: A modern synthesis. McGraw-Hill, New York.

----. 1980. Drought, stress and the origin of adaptations. p. 7–20. *In* N.C. Turner and P.J. Kramer (ed.) Adaptation of Plants to Water and High Temperature Stress. John Wiley and Sons, New York.

Krasavtsev, O.A. 1962. Fluorescence of woody plant cells in the frozen state. Soviet Plant Physiol. (Engl. Transl.) 9:282–288.

Larcher, W., U. Heber, and K.A. Santarius. 1973. Limiting temperatures for life functions. p. 195–231. *In* H. Precht et al. (ed.) Temperature and life. Springer-Verlag New York, New York.

Larque-Saavedra, A., and G.M.T. Rodriguez. 1979. Maternal inheritance of abscisic acid (ABA) in *Zea mays* L. p. 23. *In* Abstracts of the 10th International Conference on Plant Growth Substances. Madison, WI.

Larter, E.N. 1973. Progress in the development of Triticale in Canada. p. 69–74. *In* R. MacIntyre and M. Campbell (ed.) Triticale, Proceedings International Symposium, El Baton, Mexico. 1–3 October.

Lawlor, D.W. 1979. Effects of water and heat stress on carbon metabolism of plants with C_3 and C_4 photosynthesis. p. 304–326. *In* H. Mussell and R.C. Staples (ed.) Stress physiology in crop plants. John Wiley and Sons, New York.

Legge, W.G. 1979. The cold hardiness of tillers of acclimated winter wheat (*Triticum aestivum* L.) plants. M.Sc. thesis. Univ. of Saskatchewan, Saskatoon.

----, D.B. Fowler, and L.V. Gusta. 1983. The cold hardiness of winter wheat tillers acclimated under field conditions. Can. J. Plant Sci. 63:879–888.

Levitt, J. 1956. The hardiness of plants. Academic Press, New York.

----. 1980a *In* Responses of Plants to Environmental Stress, Vol. 1. 2nd ed. Academic Press, New York.

----. 1980b. Responses of Plants to Environmental Stress, Vol. 2. 2nd ed. Academic Press, New York.

Limin, A.E., and D.B. Fowler. 1982. The expression of cold hardiness in *Triticum* species amphiploids. Can. J. Genet. Cytol. 24:51–56.

----, and ----. 1983. Genetics of cold hardiness. p. 193–207. *In* D.B. Fowler et al. (ed.) New frontiers in winter wheat production. Division of Extension and Community Relations, University of Saskatchewan, Saskatoon.

Lin, C.Y., J.K. Roberts, and J.L. Key. 1984. Acquisition of thermotolerance in soybean seedlings. Synthesis and accumulation of heat shock proteins and their cellular localization. Plant Physiol. 74:152–160.

Lindlow, S.E. 1983. The role of bacterial ice nucleation in frost injury to plants. Ann. Rev. Phytopathol. 21:363–384.

----, D.C. Arny, W.R. Barchet, and C.D. Upper. 1978. The role of bacterial ice nuclei in frost injury to sensitive plants. p. 249–263. *In* P.H. Li and A. Sakai (ed.) Plant cold hardiness and freezing stress. Academic Press, New York.

----, ----, and C.D. Upper. 1982. Bacterial ice nucleation: A factor in frost injury to plants. Plant Physiol. 709:1084–1089.

Lomas, J., and Y. Shoshoua. 1974. The dependence of wheat yields and grain weight in a semi-arid region on rainfall and on the number of hot, dry days. Isr. J. Agric. Res. 23:113–121.

Mansfield, T.A., A.R. Wellburn, and T.J.S. Moreira. 1978. The role of abscisic acid and farnesol in the alleviation of water stress. Philos. Trans. R. Soc. London B 284:471–482.

Marcellos, H. and M.J. Burke. 1979. Frost injury in wheat: Ice formation and injury in leaves. Aust. J. Plant Physiol. 6:513–521.

----, and W.V. Single. 1976. Ice nucleation on wheat. Agric. Meterol. 16:125–129.

Martineau, J.R., J.E. Specht, J.H. Williams, and C.Y. Sullivan. 1979. Temperature tolerance in soybeans. I. Evaluation of technique for assessing cellular membrane thermostability. Crop Sci. 19:75–78.

Mayoral, M.L., D. Atsmon, D. Shimshi, and Z. Gromet-Elhanan. 1981. Effect of water stress on enzyme activities in wheat and related wild species: Carboxylase activity, electron transport and photophosphorylation in isolated chloroplasts. Aust. J. Plant Physiol. 8:385–393.

McKeon, T.A., N.E. Hoffman, and S.F. Yang. 1982. The effect of plant hormone pretreatments on ethylene production and synthesis of 1-amionocyclopropane-1-carboxylic acid in water-stressed wheat leaves. Planta 155:437–443.

McMichael, B.L., W.R. Jordan, and R.D. Powell. 1972. An effect of water stress on ethylene production by intact cotton petioles. Plant Physiol. 49:658–660.

McWilliam, J.R. 1980. Adaptation to high temperature stress. p. 444–447. *In* N.C. Turner and P.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Mendoza, H.A., and R.N. Estrada. 1979. Breeding potatoes for tolerance to stress: Heat and frost. p. 227–262. *In* H. Mussell and R.C. Staples (ed.) Stress physiology in crop plants. John Wiley and Sons, New York.

Milborrow, B.V. 1974. The chemistry and physiology of abscisic acid. Annu. Rev. Plant Physiol. 25:259–307.

----. 1979. Antitranspirants and the regulation of abscisic acid content. Austr. J. Plant Plysiol. 6:249–254.

----, and R.C. Noddle. 1970. Conversion of 5-(1.2-epoxy-2,6,6- trimethycyclohexyl)-3-methylpenta-*cis*-2-*trans*-4-dienoic acid into abscisic acid in plants. Biochem. J. 199:727–734.

Miller, R.W., I. de la Roche, and M.K. Pomeroy. 1974. Structural and functional responses

of wheat mitochondrial membranes to growth at low temperatures. Plant Physiol. 53:426–433.

Mizrahi, Y., S.G. Scherings, S. Malis Arad, and A.E. Richmond. 1974. Aspects of the effect of ABA on the water status of barley and wheat seedlings. Physiol. Plant. 31:44–50.

Morgan, J.M. 1977. Differences in osmoregulation between wheat genotypes. Nature (London) 270:234–235.

----. 1980a. Possible role of abscisic acid in reducing seed set in water-stressed wheat plants. Nature (London) 285:655–657.

----. 1980b. Osmotic adjustment in the spikelets and leaves of wheat. J. Exp. Bot. 31:655–665.

Munns, R., C.J. Brady, and E.W.R. Barlow. 1979. Solute accumulation in the apex and leaves of wheat during water stress. Aust. J. Plant Physiol. 6:379–389.

----, and R. Weir. 1981. Contribution of sugars to osmotic adjustment in elongating and expanded zones of wheat leaves during moderate water deficits at two light levels. Aust. J. Plant Physiol. 8:93–105.

Mussell, H., and R.C. Staples (ed.). 1979. Stress physiology in crop plants. John Wiley and Sons, New York.

Naas, H.G., and J.D.E. Sterling. 1981. Comparison of tests characterizing varieties of barley and wheat for moisture stress resistance. Can. J. Plant Sci. 61:283–292.

Ogunkanmi, A.B., A.R. Wellburn, and T.A. Mansfield. 1974. Detection and preliminary identification of endogenous antitranspirants in water-stressed *Sorghum* plants. Planta 117:293–302.

Olien, C.R. 1961. A method of studying stresses occurring in plant tissue during freezing. Crop Sci. 1:26–28.

----. 1967. Freezing stresses and survival. Annu. Rev. Plant Physiol. 18:387–408.

----. 1969. Freezing stresses in barley. p. 356–363. *In* Barley Genetics II; Proceedings of Second International Barley Genetics Symposium, Pullman, WA, R.A. Nilan (ed.) 1 Sept., 1970, Washington State University, Pullman.

----. 1981. Analysis of midwinter freezing stress. p. 35–59. *In* C.R. Olien and M.N. Smith (ed.) Analysis and improvement of plant cold hardiness. CRC Press, Boca Raton, FL.

----, B.L. Marchetti, and E. Chomyn. 1968. Ice structure in hardened winter barley. Mich. Agric. Exp. Stn. Q. Bull. 50:440–448.

Onweume, I.C., H.M. Laude. 1972. Heat-induced growth retardation and attempts at its prevention in barley and wheat coleoptiles. J. Agric. Sci. 79:331–333.

Orlyuk, A.P. 1976. Transgressive variability in winter wheat and its application in breeding. Sov. Genet. (Engl. Transl.) 12(2):129–136.

Passioura, J.B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745–752.

Pauli, A.W. 1960. Relation of crown tissue to winter survival in winter wheat. Agron. J. 52:265–266.

Paulsen, G.M. 1968. Effect of photoperiod and temperature on cold hardening in winter wheat. Crop Sci. 8:29–32.

Pearcy, R.W., J.A. Berry, and D.C. Fork. 1977. The effects of growth temperature on the thermal stability of the photosynthetic apparatus of *Atriplex lentiformis* (Torr.) Wats. Plant Physiol. 59:873–878.

Pheloung, P., and E.W.R. Barlow. 1981. Respiration and carbohydrate accumulation in water-stressed wheat apex. J. Exp. Bot. 32:921–931.

Pomeroy, M.K., C.J. Andrews, and G. Fedak. 1975. Cold hardening and dehardening responses in winter wheat and winter barley. Can. J. Plant Sci. 55:529–535.

----, and D. Siminovitch. 1971. Seasonal cytological changes in secondary phloem parenchyma cells in *Robinia pseudoacacia* L. in relation to cold hardiness. Can. J. Bot. 49:787–795.

Powell, D.B.B. 1978. Regulation of plant water potential by membranes of the endodermis in young roots. Plant Cell Environ. 28:192–203.

Quarrie, S.A. 1980. Genotypic differences in leaf water potential, abscisic acid and proline concentrations in spring wheat during drought stress. Ann. Bot. 46:383–394.

----. 1981. Genetic variability and heritability of drought-induced abscisic acid accumulation in spring wheat. Plant Cell Environ. 4:147–151.

----. 1982. Droopy: A wilty mutant of potato deficient in abscisic acid. Plant Cell Environ. 5:23–26.

----, and I.E. Henson. 1982. Biparental inheritance of drought-induced accumulation of abscisic acid in wheat and pearl millet. Ann. Bot. 49:265–268.

----, and H.G. Jones. 1977. Effects of abscisic acid and water stress on development and morphology of wheat. J. Exp. Bot. 28:192–203.

Quisenberry, K.S., and L.P. Reitz. 1974. Turkey wheat: The cornerstone of an empire. Agric. Hist. 48:98–114.

Quisenberry, J.E. 1982. Breeding for drought resistance and plant water use efficiency. p. 193–212. *In* M.N. Christiansen and C.F. Lewis (ed.) Breeding plants for less favorable environments. John Wiley and Sons, New York.

Raison, J.K., and J.A. Berry. 1979. Viscotropic denaturation of chloroplast membranes and acclimation to temperature by adjustment of lipid viscosity. p. 149–152. Carnegie Inst. Annual Report of the Director, Dept. of Plant Biology.

Rajashekar, C., L.V. Gusta, and M.J. Burke. 1980. Membrane structural transition: Probable relation to frost damage in hardy herbaceous species. p. 255–274. *In* J.M. Lyons et al. (ed.) Low temperature stress in crop plants. Academic Press, New York.

Richards, R.A., and J.B. Passioura. 1981. Seminal root morphology and water use of wheat. I. Environmental Effects. Crop Sci. 21:249–252.

Saini, H.S., and D. Aspinall. 1981. Effect of water deficit on sporogenesis in wheat (*Triticum aestivum* L.) Ann. Bot. 48:623–644.

----, and ----. 1982a. Abnormal sporogenesis in wheat (*Triticum aestivum* L.) induced by short period of high temperature. Ann. Bot. 49:835–846.

----, and ----. 1982b. Sterility in wheat (*Triticum aestivum* L.) induced by water deficit or high temperature: Possible mediation by abscisic acid. Aust. J. Plant Physiol. 9:529–537.

----, M. Sedgley, and A. Aspinall. 1983. Effect of heat stress during floral development on pollen tube growth and ovary anatomy in wheat (*Triticum aestivum* L.) Aust. J. Plant Physiol. 10:137–144.

Salcheva, G., and G. Samygin. 1963. A microscopic study of freezing of the tissues of winter wheat. Fiziol. Rast. 10:65–72.

Salmon, S.C. 1933. Resistance of varieties of winter wheat and rye to low temperature in relation to winter hardiness and adaptation. Kansas Agric. Exp. Stn. Tech. Bull. 35:1–66.

Santarius, K.A., and M. Muller. 1979. Investigation on heat resistance of spinach leaves. Planta 146:529–538.

Sarvis, J.T., and J.C. Thysell. 1936. Crop rotations and tillage experiments at the Northern Great Plains Field Station, Mandan, North Dakota. USDA Tech. Bull. 536. U.S. Government Printing Office, Washington, DC.

Shelepov, V.V., O.A. Kul'chitsbaya, and V.I. Shelepova. 1980. Breeding winter bread wheat for winter hardiness in the south of the Ukraine. Plant Breed. Abstr. 50:8397 (abstr.).

Shimshi, D., and J. Ephrat. 1975. Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis, and yield. Agron. J. 67:326–331.

----, M.L. Mayoral, and D. Atsmon. 1982. Responses to water stress in wheat and related wild species. Crop Sci. 22:123–128.

Siminovitch, D., G.F. Gfeller, and B. Rheaume. 1967. The multiple character of the biochemical mechanism of freezing resistance in plant cells. p. 93–117. *In* E. Asahina (ed.) Cellular injury and resistance in freezing organisms. The Institute of Low Temperature Science, Hokkaido University.

----, and G.W. Scarth. 1938. A study of the mechanism of frost injury to plants. Can. J. Res. (C) 16:467–481.

Single, W.V. 1964. Studies on frost injury to wheat. II. Ice formation within the plant. Aust. J. Agric. Res. 15:869–875.

----, and H. Marcellos. 1974. Studies on frost injury to wheat. IV. Freezing of ears after emergence from the leaf sheath. Aust. J. Agric. Res. 25:679.

Smika, D.E., and R.W. Shawcroft. 1980. Preliminary study using a wind tunnel to determine the effect of hot wind on a wheat crop. Field Crops Res. 3:129–135.

Steponkus, P.L., M.F. Dowgert, R.Y. Evans, and W.J. Gordon-Kammin. 1982. Cryobiology of isolated protoplast. p. 459–474. *In* P.H. Li and A. Sakai. (ed.) Plant cold hardiness and freezing stress. Mechanism and Crop Implications, Vol. 2. Academic Press, New York.

Stevens, M.A., and J. Rudich. 1978. Genetic potential for overcoming physiological limitations on adaptability, yield and quality in the tomato. Hortic. Sci. 13(6):673–678.

Stewart, C.R., and A.D. Hanson. 1980. Proline accumulation as a metabolic response to water stress. p. 173–189. *In* N.C. Turner and P.J. Kramer (ed.) Adaptation of Plants to water and high temperature stress. John Wiley and Sons, New York.

Stushnoff, C., D.B. Fowler, and A. Brule-Babel. 1983. Breeding and selection for resistance to low temperature. p. 115–136. *In* P.B. Vose (ed.) Plant breeding—A contemporary basis. Pergamon, London.

Sullivan, C.Y., and W.M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. p. 263–281. *In* H. Mussell and R.C. Staples (ed.) Stress physiology in crop plants. John Wiley and Sons, New York.

Svec, L.V., and H.F. Hodges. 1972. Cold hardening and morphology of barley seedlings in controlled and natural environments. Can. J. Plant Sci. 52:955–963.

Tal, M., D. Imber, and I. Gardi. 1974. Abnormal stomatal behaviour and hormonal imbalance in flacca, a wilty mutant of tomato: Effect of abscisic acid and auxin on stomatal behaviour and peroxidase activity. J. Exp. Bot. 25:51–60.

Tan, B.H., and G.M. Halloran. 1982. Variation and correlations of proline accumulation in spring wheat cultivars. Crop Sci. 22:459–463.

Thomas, J.B., and D.A. Gaudet. 1983. The winter wheat breeding program at Lethbridge: Some ideas and approaches. p. 208–227. *In* D.B. Fowler et al. New frontiers in winter wheat production. Division of Extension and Community Relations, University of Saskatchewan, Saskatoon.

Townley-Smith, T.F., and E.A. Hurd. 1979. Testing and selecting for drought resistance in wheat. p. 447–464. *In* H. Mussell and R.C. Staples (ed.) Stress physiology in crop plants. John Wiley and Sons, New York.

Treshow, M. (ed.) 1970. Environment and plant response. McGraw-Hill, New York.

Turner, N.C., and M.M. Jones. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. p. 87–103. *In* N.C. Turner and P.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

----, and P.J. Kramer. 1980. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Uemura, M., and S. Yoshida. 1984. Involvement of plasma membrane alterations in cold acclimation of winter rye (*Secale cereale* L. cv. Puma). Plant Physiol. 75:818–826.

Walton, D.C. 1980. Biochemistry and physiology of abscisic acid. Ann. Rev. Plant Physiol. 31:453–489.

Wardlaw, I.F. 1971. The early stages of grain development in wheat: Response to water stress in a single variety. Aust. J. Biol. Sci. 24:1047–1055.

Weidner, M., and C. Ziemens. 1975. Preadaptation of protein synthesis in wheat seedlings to high temperature. Plant Physiol. 56:590–594.

Wright, S.T.C. 1969. An increase in the "Inhibitor-β" content of detached wheat leaves following a period of wilting. Planta. 86:10–20.

----. 1977. The relationship between leaf water potential (ψ leaf) and the levels of abscisic acid and ethylene in excised wheat leaves. Planta 134:183–189.

----. 1978. Phytohormones and stress phenomena. p. 495–536. *In* D.S. Letham et al. (ed.)

Phytohormones and related compounds–A comprehensive treatise, Vol. 2. Elsevier, Amsterdam.

----. 1980. The effect of plant growth regulator treatments on the levels of ethylene emanating from excised turgid and wilted wheat leaves. Planta 148:381–388.

----, and R.W.P. Hiron. 1969. (+)-Abscisic acid, the growth inhibitor induced in detached wheat leaves by a period of wilting. Nature (London) 224:719–720.

5 Origins and Analyses of Genes and Genomes in Wheat and Its Relatives

Rosalind Morris

A. Evolution in the Genus *Triticum* and the Origin of Cultivated Wheat
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B. The Molecular Genetics of Wheat: Toward an Understanding of 16 Billion Base Pairs of DNA
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5 Origins and Analyses of Genes and Genomes in Wheat and Its Relatives

Rosalind Morris, ***coordinator***

The classical genetic and cytogenetic foundations of wheat and related species were established during the 50 years before the publication of the first edition of this monograph in 1967. Investigations along these lines have continued into the 1980s and have been enhanced by improved methods for determining genome relationships and for mapping genes. Chromosome banding, a cytological tool developed in the 1970s, has introduced a new dimension in the identification of individual chromosomes. The aneuploid methods that have been applied so successfully to associate genes with chromosomes in hexaploid wheat species, have been adapted for use also in tetraploid wheat species.

This wellspring of genetic and cytogenetic information has provided a framework for rapid and significant developments in molecular and biochemical genetics as applied to wheat and its relatives. We are on the threshold of being able to characterize wheat genes and genomes not solely by their phenotypic effects but also by their molecular structure and behavior. This knowledge provides exciting prospects for expanding the traditional ways of transferring genes by crossing over or chromosome rearrangements, to include manipulation at the molecular level. The role of the cytoplasm in wheat heredity is being elucidated by molecular studies on chloroplast and mitochondrial DNAs. Refinements in biochemical techniques have facilitated studies on enzymatic and nonenzymatic proteins in the Triticeae. The chromosomal locations of enzyme structural genes are being used to determine homologies of chromosomes and chromosome arms among the genomes of wheat and other species. Dissection of the gluten protein of wheat endosperm into its component fractions and studies of the genetic and biochemical properties of these fractions, have practical implications in identifying wheat cultivars and improving bread quality.

In order to provide up-to-date and adequate coverage of these diverse

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yet related avenues to a holistic view of wheat as well as alien genes and genomes, this chapter has been divided into eight sections, each written by one or more authorities on the topic.

5A Evolution in the Genus *Triticum* and the Origin of Cultivated Wheat

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5A–1 GENOMIC ANALYSIS IN THE TRITICEAE

The determination of evolutionary relationships on the basis of chromosome pairing in hybrids was first accomplished by Rosenberg (1909) in the genus *Drosera*. This method, termed *genomic analysis*, was elegantly and exhaustively employed by Kihara and his colleagues (see review by Lilienfeld, 1951) and led to an essentially correct picture of the evolutionary and species relationships in the genus *Triticum* as defined by Morris and Sears (1967).

Ideally, the process of genomic analysis involves the production of triploid hybrids between allotetraploids and their putative diploid ancestors. The occurrence of the basic (diploid) number of bivalents in the triploid hybrid is taken as an indication of genomic homology (virtual identity) of the chromosomes of the diploid parent with those of one genome of the allotetraploid. This form of genomic analysis measures the total amount of chromosome pairing per cell. The determination of genomic homology becomes more difficult when there are not exactly the basic number of bivalents, when multivalents are observed, or when tetraploid or high-ploidy hybrids must be analyzed. Usually, reductions in total chromosome pairing are assumed to indicate some differentiation of otherwise identical genomes (i.e., becoming no longer homologous but homoeologous), and multivalents are taken to demonstrate residual homology or translocation heterozygosity. The interpretation of data derived from high-polyploidy hybrids is even more equivocal.

Other methods for determining genomic relationships in the genus *Triticum* also have been employed. The method used necessarily affects

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the reliability of the results obtained. Since all the methods are, in fact, vicariously comparing the DNA (either nuclear or cytoplasmic) of one species with another, then the technique which provides measures of the similarity of the greatest proportion of the DNA should be the most reliable.

The self-fertility of alloplasmic lines has been used to provide evidence allowing the recognition of the maternal parent in allopolyploids in the wheat group (Maan, 1973; Tsunewaki, 1980). In addition, Ogihara and Tsunewaki (1982, 1984) have made restriction-enzyme analyses of the chloroplasts of most of the *Triticum* spp. Most polyploids and their related diploids showed identical restriction patterns. Such results are both clear and unequivocal; however, they are based on an extremely small percentage of the total DNA in the cell. In addition, since Adams and Rothman (1982) have shown that the cleavage sites of restriction enzymes are not randomly distributed, indications of phylogenetic relationships using restriction-enzyme data may be biased. Clearly, the characteristics of the cytoplasms are controlled by a relatively small number of genes; further, the DNA of the chloroplast cannot contain many loci. Consequently, the probability of fortuitous similarity or dissimilarity is increased, together with an increase in the probability of convergent evolution rather than common descent.

Similarly clear, and sometimes contradictory, results are obtained from immunochemical reactions and electrophoretic studies. For example, Aniol (1974) and Jaaska (1976) used immunochemical and electrophoretic methods, respectively, and observed similarity between the *T. speltoides* genome and the B genome of tetraploid wheat. Also, mainly following a study of electrophoretic banding patterns, Johnson (1975) proposed that the B genome derives from *T. urartu*, a species with a now-undoubted A genome.

The differential staining of heterochromatin, DNA hybridization, and other methods that mostly recognize repeated DNA sequences provide very clear and frequently beautiful patterns from which homology may be inferred. However, the very clarity of the preparations tends to obscure the fact that: (i) the same sequences can appear at several locations throughout the genome; (ii) the same sequences can often be found in distant nonlineal taxa; and (iii) some 95% or more of the DNA may not be detected and consequently not be considered in the phylogenetic conclusions that are drawn. These and other techniques make powerful tools for characterizing individual chromosomes, and the more bands identified or sites recognized, the more reliable the identification. However, the mere presence or absence of a particular band at a site does not mean that reliable evolutionary conclusions can be drawn.

Karyotype analysis tends to suffer from the technical problems associated with the derivation of the data (Larsen and Kimber, 1973) and consequently may lack both objective and subjective accuracy. Use of the absolute length of chromosomes in the determination of phylogenetic

relationships is generally a very unreliable technique because of differences in contraction from cell to cell. Measurements of relative length are somewhat better; however, Schlegel and Mettin (1978) have shown that in *T. aestivum* measurements of the four chromosomes of the two more similar pairs in about 100 cells would be necessary to differentiate between homologues and nonhomologues with a probability of 0.99. Arm ratio is more reliable (Kimber, 1971) particularly when strongly heterobrachial chromosomes are present. However, observation of two chromosomes with the same arm ratio in two different species does not of itself demonstrate homology or even homoeology.

Phylogenetic relationships of the wheats and other plant groups, based mainly on the morphological characteristics of the putative relatives, have proved to be largely correct. The recognition of a cluster of characteristics as the mode for an individual taxon and the identification of similar clusters for species thought to be related represent an assessment of many loci and consequently are usually reasonably reliable. In some cases in the wheat group, however, morphological comparisons may not be good indicators of phylogenetic relationships; e.g., Vardi (1973) has shown the introgression of characteristics to and from diploid progenitors. In addition, Kimber (1983) has described the suppression of characters of generic importance in wide crosses involving polyploids in the Triticeae.

Recently, Kimber and associates (Alonso and Kimber, 1981, 1983a, 1983b; Espinasse and Kimber, 1981; Kimber and Alonso, 1981; Kimber et al., 1981) have developed numerical methods for the analysis of chromosome pairing in hybrids and the consequent determination of genomic relationships. The essential features of these techniques are the calculation of a measure of how often the chromosomes pair (mean arm-pairing frequency, c) and a measure of the similarity of two or more of the genomes present (relative affinity, x). The value of c (which is not the same as chiasma frequency) is obtained from the frequencies of the observed meiotic figures (Alonso and Kimber, 1981); it ranges from 0.0, when there is no chromosome pairing at all, to 1.0, when every possible arm is paired in every cell. The frequencies expected of the various meiotic figures are calculated on the basis of various assumptions of synapsis, chiasma formation, and the relative affinity of the genomes present (Alonso and Kimber, 1981). The relative affinity (x) ranges from 0.5, when all the genomes are equally related to each other, to 1.0, when two or more genomes pair to the exclusion of all other genomes. These assumptions and definitions result in various models of chromosome pairing at increasing levels of ploidy. At the triploid level two models are expected: First, the 3:0 model where all three genomes are equally related, and second, the 2:1 model where two of the genomes are more closely related to each other and are equally and more distantly related to the third. Similarly, four models are considered at the tetraploid level designated 4:0, 2:2, 2:1:1, and 3:1, and at the pentaploid level there are six models, designated 5:0, 2:2:1, 2:1:1:1, 3:2, 3:1:1, and 4:1. The optimum value of

the relative affinity is calculated (by minimum sums of squares of differences between observed and expected pairing) for each of the appropriate models. The model that fits the observed data best, its associated value of x, and the observed value of c are taken to describe the evolutionary relationships of the species involved.

Studies of genomic relationships based on this type of numerical analysis differ from the classical method by considering not only the amount but also the pattern of chromosome pairing. Exclusive consideration of the value of c is simply a quantification of the method of Kihara and his co-workers. Together with the values of c and x, the determination of which pairing pattern fits best adds another dimension to recognizing the relationships of the chromosomes and thus the genomes present in the hybrid. Both classical genomic analysis and these numerical methods are based on a comparison of some DNA at virtually every locus along the homologous or homoeologous chromosomes present. Consequently, it is to be expected that they will provide the most reliable data upon which to base phylogenetic conclusions.

5A–2 ASSIGNMENT OF GENOME SYMBOLS

5A–2.1 Diploids

A classification of the *Triticum* diploids on the basis of the genome relationships of the species was first made by Kihara (see Lilienfeld, 1951, for review). Nine diploid species were recognized, some of which were thought to carry genomes somewhat modified from other, closely related diploids.

The most homogeneous group consists of the S-genome species: *T. speltoides*, *T. longissimum*, and *T. bicorne*. These species and their various subspecies have a similar morphology, can intercross, and have overlapping distributions. The second group of species, to whose genomes Kihara assigned the letter C (Table 5A–1), consists of two species, *T. dichasians* (C) and *T. umbellulatum* (C^u), that are morphologically distinct, contrasting in this respect with the S-genome group. Recently, Kimber and Abu Bakar (1981) have shown that the C and C^u genomes are no more closely related to each other than either is to any other genome tested (S, M, and D). Consequently, these authors have proposed that the designation of the genome of *T. umbellulatum* be changed to U (Table 5A–1).

The third group of diploids, designated the M group by Kihara, is by far the most heterogeneous. Four species, *T. comosum*, *T. uniaristatum*, *T. tauschii*, and *T. tripsacoides*, are recognized; Kihara assigned the symbols M, M^u, D, and Mt, respectively, to the four genomes. *Triticum tauschii* is distinct from the remaining species of this group. There is some doubt that it should be included at all, as is implicitly recognized by the assignment of the symbol D. The superscript *u* in the genome

Table 5A–1. The proposed genome symbols of the diploid species of *Triticum*. (Kimber and Sears, 1983.)

Species	Symbol	Synonyms
T. monococcum L.	A	*T. boeoticum, T. urartu*
T. speltoides (Tausch) Gren. ex Richter	S	*Ae. speltoides*
T. bicorne Forsk.	S^b	*Ae. bicornis*
T. longissimum (Schweinf. & Muschli in Muschli) Bowden	S^l	*Ae. longissima, Ae. sharonensis*
T. searsii (Feldman & Kislev) Feldman, comb. nov.	S^s	*Ae. searsii*
T. tripsacoides (Jaub. & Spach) Bowden	Mt	*Ae. mutica*
T. tauschii (Coss.) Schmal.	D	*Ae. squarrosa*
T. comosum (Sibth. & Sm.) Richter	M	*Ae. comosa, Ae. heldrechii*
T. uniaristatum (Vis.) Richter	Un	*Ae. uniaristata*
T. dichasians (Zhuk.) Bowden	C	*Ae. caudata*
T. umbellulatum (Zhuk.) Bowden	U	*Ae. umbellulata*

symbol of *T. uniaristatum* indicates that it is a modified M genome from *T. comosum*; however, Kimber et al. (1983) have shown that the M^u genome of *T. uniaristatum* is no closer to the M genome of *T. comosum* than it is to any other genome tested (D, U, and S). The symbol Un is therefore proposed for the designation of the genome of *T. uniaristatum* (Table 5A–1).

The remaining species of Kihara's M group of diploids, *T. tripsacoides*, not only is morphologically distinct from the other diploids of the M group, but is quite distinct from all the other *Triticum* diploids. It is also the only distinct genome in the diploids not found in any polyploid. In addition, there has been considerable confusion in the literature concerning its genome symbol, caused partly by its inclusion in the M group of diploids. The symbol assigned to this species is Mt and not M^t (see Table 6 in Lilienfeld, 1951, for example). Consequently, there is not the intent to indicate a modified M genome but actually a totally different genome. Kimber (1982) has shown by numerical genome analysis that the Mt genome of *T. tripsacoides* is not homologous to the A, B, D, M, or U genomes.

5A–2.2 Polyploids

The assignment of the genomes present in the polyploid forms of the genus has been made largely on the basis of cytological and morphological evidence. The 17 polyploid species, subspecies, and ploidy forms in the genus as listed by Morris and Sears (1967) contain a total of 40 genomes. Only 21 of these have been identified on the basis of classical genomic analysis, and 17 more by numerical genomic analysis. The remaining genomes are allocated on the basis of morphological comparisons. Even the genomes that are assigned on the basis of chromosome pairing appear in some cases to have been substantially modified in the polyploid. Clearly,

many new hybrids and analyses need to be made. The genome symbols of the polyploid species of *Triticum* are given in Table 5A–2.

5A–3 EVOLUTION OF CULTIVATED WHEATS

It has long been known from the work of Sakamura (1918), Kihara (1919, 1924), Sax (1922), and others that the cultivated wheats constitute an allopolyploid series, diploid through hexaploid. In the early view it was assumed that first an ancestral diploid had differentiated into various other diploids, including diploid wheat (with genome A). Then a second species (with genome B), whose chromosomes were believed to have become strongly differentiated structurally from those of genome A, was combined with A to form tetraploid wheat. Similarly, a presumed highly differentiated genome D was added to the tetraploid AABB to form hexaploid wheat AABBDD.

By 1967, when the first edition of *Wheat and Wheat Improvement* was published, it was already clear that genomes A, B, and D were nowhere near as highly differentiated as had been believed. It has been established (Sears, 1966b; Sears and Okamoto, 1956) that each chromosome of hexaploid wheat has a homoeologue in each of the other two genomes to which it is closely related genetically. Okamoto (1957) and Riley and Chapman (1958) had discovered that meiotic pairing in hex-

Table 5A–2. The proposed genome symbols of the polyploid species of the genus *Triticum*. Underlining of symbols indicates substantial modification of the genome concerned. (Kimber and Sears, 1983.)

Species	Genomes	Synonyms
T. turgidum L.	AB	*T. carthlicum, T. dicoccoides, T. dicoccon, T. dicoccum, T. durum, T. polonicum*
T. timopheevii (Zhuk.) Zhuk.	AG	*T. araraticum*
T. zhukovskyi Men. & Er.	AAG	*T. timopheevii* var. *zhukovskyi*
T. aestivum L.	ABD	*T. compactum, T. macha, T. spelta, T. sphaerococcum, T. vavilovii*
T. ventricosum Ces.	DUn	*Aegilops ventricosa*
T. crassum (4x) (Boiss.) Aitch. & Hensl.	DM	*Ae. crassa*
T. crassum (6x) (Boiss.) Aitch. & Hensl.	DDM	*Ae. crassa*
T. syriacum Bowden	DMS	*Ae. crassa* ssp. *vavilovii, Ae. vavilovii*
T. juvenale Thell.	DMU	*Ae. juvenalis*
T. kotschyi (Boiss.) Bowden	US	*Ae. kotschyi, Ae. peregrina, Ae. variabilis*
T. ovatum (L.) Raspail	UM	*Ae. ovata*
T. triaristatum (4x) (Willd.) Godr. & Gren.	UM	*Ae. triaristata*
T. triaristatum (6x) (Willd.) Godr. & Gren.	UMUn	*Ae. triaristata*
T. machrochaetum (Schuttl. & Huet. ex Duval-Jouve) Richter	UM	*Ae. biuncialis, Ae. lorentii*
T. columnare (Zhuk.) Morris & Sears	UM	*Ae. columnaris*
T. triunciale (L.) Raspail	UC	*Ae. triuncialis*
T. cylindricum Ces.	CD	*Ae. cylindrica*

aploid wheat is sufficiently suppressed by a gene or genes on the long arm of chromosome 5B that only homologues can pair; in the absence of chromosome 5B, considerable pairing occurs between homoeologues. Thus the polyploid wheats were shown to be more auto- than allopolyploid but to behave cytologically like diploids and thereby to maintain a high level of fertility and stability.

Besides the gene for suppression of pairing on chromosome 5B (designated *Ph* by Wall et al., 1971) and subsequently modified to *Ph1*, other suppressors, relatively minor in effect, have been found on 3DS (Mello-Sampayo, 1968, 1971; Mello-Sampayo and Canas, 1973; Upadhya and Swaminathan, 1967), 3AS (Driscoll, 1973; Upadhya and Swaminathan, 1967), and 4D (Driscoll, 1973). Promoters of pairing exist on 5BS (Feldman and Mello-Sampayo, 1967; Riley and Chapman, 1967), 5DL (Feldman, 1966a; Riley et al., 1966), 5DS (Feldman, 1968), and 5AL (Feldman, 1968). Thus, the control of meiotic pairing in wheat is genetically much more complex than it first appeared, with the level of pairing depending on the balance between several suppressors and several promoters (Feldman, 1968). Nevertheless, the gene *Ph1* on 5BL is much more effective than any of the others and is often referred to as *the* pairing-control gene. In the absence of *Ph1* the remaining suppressors roughly balance the various promoters, providing a pairing level approximately the same as would be expected in a raw allohexaploid involving genomes A, B, and D. Thus *Ph1* may be considered the critical pairing-control gene—the only one capable of switching the pairing level from that of the original polyploid to a pairing level characteristic of diploids.

Genes promoting pairing clearly exist in at least some of the diploid relatives of wheat (see Sears, 1976, for review). Suppressors also occur in certain diploids (Feldman, 1979; Maan, 1977; Okamoto and Inomata, 1974; Waines, 1976), and suppression of pairing is associated with the accessory chromosomes of *T. speltoides* and *T. tripsacoides* (Dover and Riley, 1972). Whether *Ph1* was obtained by wheat from a diploid species or arose by mutation after the synthesis of tetraploid wheat is not known, but a mutational origin is supported by the strong selection pressure that would have existed in the raw AABB amphidiploid, favoring diploid-like meiotic behavior.

From the strong morphological similarities between diploid wheat, *T. monococcum*, and tetraploid wheat, *T. turgidum*, and from the chromosome pairing observed in hybrids between them, it has long been clear that the A genome of the polyploid wheats must have come from *T. monococcum*. Since archaeological evidence (Helbaek, 1959) has established that *T. turgidum* was taken into cultivation at least as early as *T. monococcum* (about 8000 B.C.), there seems to be no doubt that the diploid wheat that contributed the A genome to the tetraploid was a wild form.

The source of the D genome of hexaploid wheat has likewise been clearly established; it came from *T. tauschii* (*Aegilops squarrosa*). This

was discovered by McFadden and Sears (1944, 1946) and independently by Kihara (1944), and all subsequent evidence has supported the conclusion. Involvement of either a wild or a cultivated tetraploid was possible, since cultivated forms of emmer, a tetraploid, were in existence by the time the hexaploid appeared, which was about 2000 yr later than the beginning of cultivation of emmer (Helbaek, 1959). Evidence from genes for waxiness and other characteristics (Tsunewaki, 1966) favors an origin from cultivated emmer, as does the phenotype of tetraploids extracted from hexaploid wheats by Kerber (1964) and others.

Although various suggestions as to the source of the B genome had been made earlier, the first proposal to gain wide acceptance was that of Sarkar and Stebbins (1956), who concluded that *T. speltoides* had contributed either the whole of the B genome or a substantial part of it. This conclusion, based on morphological considerations, unfortunately could not be checked cytologically, because the only strains of *T. speltoides* available at that time were strong promoters of meiotic pairing, and in hybrids of *T. speltoides* with hexaploid or tetraploid wheat there was no way of distinguishing homologous from homoeologous pairing. Eventually, however, plants of *T. speltoides* were discovered that lacked the gene or genes for high pairing, and in hybrids of these with hexaploid wheat there was little or no pairing of the *T. speltoides* chromosomes (Kimber and Athwal, 1972). This discovery re-opened the controversy concerning the source of the B genome.

Triticum longissimum was shown by Feldman (1979) to be a strong candidate for the B-genome donor, because of its suitable morphology and the relatively frequent pairing of its chromosomes with those of the B genome. However, Feldman and Kislev (1977) had already split off part of *T. longissimum* into a new species, *T. searsii*, which Feldman (1979) believes to be a more probable source of the B genome, mainly because its distribution overlaps that of both wild emmer and wild einkorn. Nath et al. (1983, 1984a) reported that DNA-hybridization data support *T. searsii* as a source of the B genome, rather than *T. longissimum* or any of its close relatives.

A proposal was made by Johnson (1975) that a diploid wheat that is often accorded specific rank as *T. urartu* was the source of the B genome. Its hybrids with other diploid wheats are sterile, but obviously not because of differentiation of its chromosomes, for in hybrids with hexaploid wheat they pair with the A-, not B-, genome chromosomes (Chapman et al., 1976; Dvořák, 1976).

On the basis of their having the genomic constitutions AA, AABB or AABBDD, all of the wild and cultivated wheats known are classifiable into three species, *T. monococcum*, *T. turgidum*, and *T. aestivum*, except the tetraploid *T. timopheevii* and the hexaploid *T. zhukovskyi*. The former has a genome G instead of B, thus being AAGG, and the latter is AAAAGG. *Triticum timopheevii* has a wild form that grows fairly widely in southeast Asia and a cultivated form that is grown only in the Caucasus region. *Triticum zhukovskyi*, a cultivated form, also grows only in the Caucasus.

There are two opposing theories concerning the origin of the G genome. One, first proposed by Wagenaar (1961), admits to no essential differences between G and B and attributes the poor chromosome pairing and sterility of *timopheevii–turgidum* hybrids to complementary genetic action. This theory has failed of confirmation in experiments measuring the pairing of individual *timopheevii* chromosomes in hybrids with wheat (Feldman, 1966b). However, the second theory, that different species contributed B and G, is not as yet supported by convincing evidence for a particular diploid as donor of the G genome. Following the demonstration of nonpairing of *T. speltoides* chromosomes with the B genome, *T. speltoides* was suggested as the G-genome donor (Shands and Kimber, 1973), but subsequent numerical analysis of additional hybrids (Kimber and Alonso, 1981; Kimber, unpublished) have failed to confirm this suggestion. Nevertheless, Nath, Thompson, and Gulati (West Virginia University, 1984, personal communication) report that DNA-hybridization data favor *T. speltoides* as the G-genome donor.

In recent years chromosomes 4A and 4B have been found to be anomalous. Okamoto (1962), who made the original assignments of chromosomes to the A and B genomes, tested what is known as 4B in hybrids with diploid wheat and observed no pairing; hence he designated it 4B, and the other group-4 chromosome he automatically called 4A. Eventual tests of 4A (Dvořák, 1983, Miller et al., 1981) showed that it also fails to pair with any einkorn chromosome. Dvořák (1983) would reverse the designations of 4A and 4B, because 4A is heavily Giemsa-banded. However, this suggestion is based on the somewhat dubious assumption that all the chromosomes of a genome should be banded to approximately the same degree. It may not be possible to decide which chromosome, if either, belongs to the B genome until the B-genome donor has been identified and shown to include a chromosome that pairs with 4A or 4B. At present, all that can be said with certainty is that neither 4A nor 4B was contributed by diploid wheat.

5A–4 EVOLUTION OF WHEAT RELATIVES

One of the clearest features of the evolution of this group of species is a reticulate pattern of relationships. Initially there must have been a diploid divergence from a seven-chromosome ancestor and then a polyploid convergence involving at least three clusters of species. In addition, it seems that genes are still being passed both up and down the polyploid series of related species. The evolution of the cluster based on the A genome is discussed in the section 5A–3 above; this section treats the remaining two, together with other aspects of the evolution of wheat relatives.

Evolution in these clusters seems to have progressed by the formation of several amphiploids with a common genome and a different second genome. Hybrids between these amphiploids have resulted in forms with

a relatively unmodified genome (the genome in common) and a repatterned genome. Zohary and Feldman (1962) proposed the terms *pivotal* for the unmodified genome and *differential* for the modified genome. The U-genome cluster contains some six or seven species (Table 5A–2), all with a pivotal genome derived from *T. umbellulatum* and with differential genomes originally derived from M-, Un-, S-, and D-genome diploids. The cytology of the interspecific hybrids was described by Feldman (1965c).

Many of the tetraploid species have sympatric distributions (Feldman 1965a; Zohary and Feldman 1962), and hybrid swarms are common. Continued hybridization between these forms often results in considerable taxonomic difficulties and a relatively swift flow of characters among the species of the group. Feldman (1965b) reported that various F_1s have a low female fertility, but that backcross progeny showed a steep increase in selfed seed set.

The D-genome cluster of species has not been as well investigated morphologically as the U-genome group. The cytology of the D-genome group is also a little different from that of the U-genome cluster. Kimber and Zhao (1983, 1984) and Zhao and Kimber (1984) have shown that the D genome is clearly unmodified in two species (*T. cylindricum* and *T. ventricosum*), somewhat modified in both the tetraploid and hexaploid *T. crassum*, and substantially modified in *T. syriacum* and *T. juvenale.* Consequently, the clear pivotal-differential pattern of the U-genome cluster is not universal in the D-genome cluster. In addition to this pattern of gene exchange among the polyploid wheat relatives, genes are also introgressed both to and from related diploids. Vardi (1973) described the production of triploid hybrids between tetraploid wheat and three diploid species. These hybrids were backcrossed with both the diploid and tetraploid parents and the introgression of characters into the recurrent parent was demonstrated.

5A–5 CONCLUSIONS

The general pattern of evolution in the wheat group is clear. It is characterized by a group of diploid species, in which there are eight distinct genomes (Table 5A-1), and a group of polyploids (tetraploid and hexaploid) in which seven of the eight diploid genomes plus two more (B and G) are found.

Axiomatically, the diploids diverged from a common seven-chromosome ancestor; consequently, the chromosomes of the diploids are homoeologous to each other and to the chromosomes found in the polyploids. The tetraploid species arose following chromosome doubling of hybrids between the diploids. Some of these allotetraploids then crossed with other diploids and the hybrids, after chromosome doubling, evolved into the hexaploid species. This dendritic pattern is overlaid by a reticulate pattern as a consequence of hybridization between polyploids and also between polyploids and diploids.

This anastomosis of relationships provides genetic and cytological pathways permitting substantial opportunity for natural introgression. There are both practical and theoretical consequences of this evolutionary situation. Practical utilization of this widely based genetic resource is relatively recent, made possible by the development of techniques for the introduction of alien variation into cultivated forms. The associated taxonomic difficulties created by the blending of characters from sympatrically distributed, but originally distinct, species represent a problem of long standing that may have no clear ultimate solution. The evolutionary development of the demonstrably successful cultivated forms of this group may well be based in several events involving introgression from related forms.

5B The Molecular Genetics of Wheat: Toward an Understanding of 16 Billion Base Pairs of DNA

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The genome of hexaploid wheat has been estimated to contain 18.1 picograms (pg) of DNA per haploid nucleus (Bennett, 1972), an amount that is equivalent to approximately 16×10^6 kilobase pairs (kb) or 16 billion base pairs (bp). More than 75% consists of repeated DNA sequences of varying degrees of reiteration and length, and a lesser proportion (20%) consists of low-copy-number or unique sequences (Smith and Flavell, 1975; Flavell and Smith, 1976; Ranjekar et al., 1976). An even smaller proportion (probably no more than 1%) consists of actual coding genes. From a molecular geneticist's point of view, coding genes can be defined as regions of DNA coding for discrete RNA products that can either have a function of their own or provide a template for the synthesis of polypeptides. In contrast to this molecular view of the wheat genome, "single" genes in plant breeding are recognized as specific phenotypes showing Mendelian inheritance. In many cases, these genes have been located on specific chromosome arms and linkage relationships are established (see section 5H, below). However, as judged from the analysis of genes controlling development in other organisms (e.g., Akam, 1983), the molecular nature of the single genes of wheat and the way in which they interact with other DNA sequences with which they are often intermingled (Rimpau et al., 1978), are likely to be complex. It is the aim

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of this section to review the progress that has been made towards understanding this complexity, the actual structure of the genes, their utilization as markers in evolutionary and plant breeding studies, and the detection of specific chromosome segments within wheat and its relatives. In addition to nuclear DNA, we also review molecular genetic studies on the DNA of chloroplasts and mitochondria.

The development of a detailed understanding of the wheat genome can be expected to have an impact on three broad areas of wheat improvement. Firstly, the understanding at a molecular level of the genes used in plant breeding may generate new approaches for the improvement of these genes. Secondly, new DNA probes will become available for tracing useful genes and chromosome segments in plant breeding. Progress in this area is particularly important for those genes that contribute to quantitative characters. Lastly, the eventual realization of molecular-genetic engineering of specific genes requires a clear understanding of their structure and the genetic environment in which they normally exist for optimum expression.

5B–1 WHEAT CHROMOSOME STRUCTURE

Cytologically, the 21 pairs of wheat chromosomes show the same morphological features as those of any other organism; namely, a primary constriction or centromere is present with secondary constrictions on two pairs of chromosomes indicating sites of ribosomal RNA genes. The length of the metaphase chromosomes is, on average, 5.6 μm (Sears, 1954) and this makes them particularly suitable for cytological analysis. (C-banding and N-banding are described in section 5E, below). The wheat nucleus itself has a volume of approximately 1700 μm^3 (assuming a diameter of 14–15 μm), in which the 2C amount of DNA (36.2 pg) is accommodated. This DNA totals 11.2 m in length, has a volume of 35 μm^3, and is subdivided into 42 chromosomes that presumably allow the DNA to be more easily controlled during cell division. This may be further facilitated by the apparently nonrandom distribution of the 42 chromosomes within the nucleus (Avivi and Feldman, 1980; Bennett, 1983). Molecular techniques are providing an array of probes that may be of use in resolving the distribution, and interrelationships within the nucleus, of centromeres, chromosome arms, and telomeres.

The DNA in the chromosomes is coiled extensively, as illustrated in Fig. 5B–1. The first level of compaction is the nucleosome. This level of folding was revealed in a number of organisms using electron microscopy and by partial digestion of nuclei with the enzyme micrococcal nuclease (for a recent review see Spiker, 1984a). In wheat, the average amount of DNA in a nucleosome is 170–185 bp (Appels, 1983; S. Spiker, personal communication, 1984) and this is typical of eukaryotes. Higher levels of DNA compaction are distributed throughout the chromosome and although heterochromatic regions may contain higher densities of DNA,

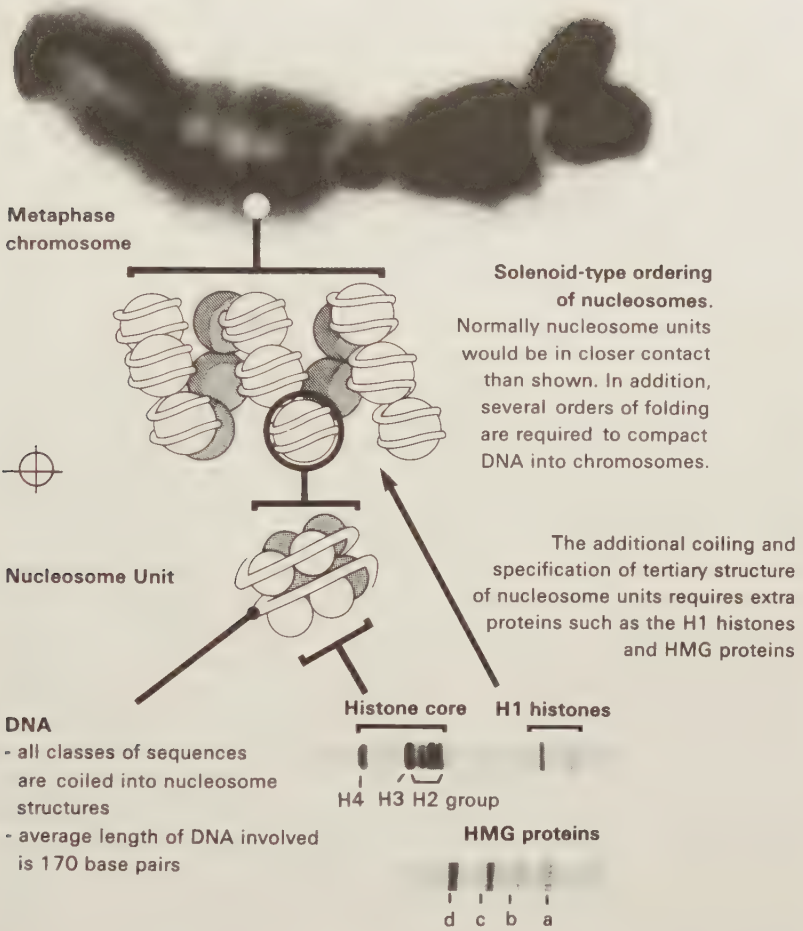

Metaphase chromosome
Solenoid-type ordering of nucleosomes. Normally nucleosome units would be in closer contact than shown. In addition, several orders of folding are required to compact DNA into chromosomes.
Nucleosome Unit
The additional coiling and specification of tertiary structure of nucleosome units requires extra proteins such as the H1 histones and HMG proteins
DNA
- all classes of sequences are coiled into nucleosome structures
- average length of DNA involved is 170 base pairs
Histone core
H1 histones
H4 H3 H2 group
HMG proteins
d c b a

Fig. 5B–1. The structure of wheat chromosomes. The wheat histone and HMG protein photographs were kindly supplied by S. Spiker and L. Arwood. Nucleosome structure is based on Finch and Klug (1976), Finch et al. (1977), and Thoma and Koller (1977). DNA is considered to wrap around the histone core in sharp bends (Richmond et al., 1984). An important part of chromosome structure that is not yet clearly understood is the form taken during DNA replication; in wheat, the whole genome is replicated within a meiotic S phase period of 3.5 h (Bennett, 1972), presumably using multiple replicons. Such replicons have been visualized in rye by DNA fiber autoradiography (Francis and Bennett, 1982) and were 20 to 25 μm in length with replication occurring at 12.1 μm/h at 23°C.

it has been shown that DNA estimations along the length of a chromosome may be rather inaccurate (Timischl and Greilhuber, 1983). It should be pointed out that the organization of DNA around the histone core and the higher levels of folding (as shown in Fig. 5B–1) have not been studied in wheat directly and may differ in detail as a result of extensive methylation of DNA. Various analyses of plant DNA have indicated a high level of methylation of cytosine residues relative to animal DNA, and in wheat 22.4% of the total cytosine residues are methylated (Wagner

Table 5B–1. Methylation of cytosine residues in wheat DNA: the distribution of 5-methyl cytosines in various nucleotide sequences (Gruenbaum et al., 1981).

Sequence	Proportion of sequence in the genome that has the C methylated
CG	82%
CA	19%
CT	19%
CC	7%
CAG	>80%
CTG	>80%
CAT	>4%

and Capesius, 1981; Table 5B–1). In animal systems, recent studies have indicated that the distribution of 5-methyl-cytosine residues is not random (for a recent example, see Church and Gilbert, 1984), which implies that these residues may be involved in controlling some aspects of gene expression. Therefore, the occurrence in wheat of this type of DNA modification may be significant at a biological level.

One aspect of higher-order chromatin structure that has been studied in wheat involves DNAase I digestion. In contrast to digestion with micrococcal nuclease, greater amounts of DNA are accessible for digestion with DNAase I, which indicates that this enzyme may be a sensitive probe for chromatin conformation, particularly in regions of active transcription. For example, Spiker et al. (1983) found that transcriptionally active regions of wheat-embryo nuclei, assayed using radioactive probes prepared from poly A^+–RNA molecules (the products of active genes), were preferentially sensitive to DNAase I. This observation indicated that in plants, as has been found in animals (Spiker, 1984a), regions of the chromatin in which transcribed DNA is located have a characteristic structure that leads to increased sensitivity of the DNA when exposed to DNAase I.

5B–1.1 Chromosomal Proteins

Even though the actual structural relationships of chromosomal proteins and DNA have not been directly determined in wheat, the chromosomal proteins themselves have been studied (Fig. 5B–1). Among the histones (Spiker and Key, 1976; Rodrigues et al., 1979; Spiker, 1982), the gene that produces the H4 histone of wheat has been sequenced (Tabata et al., 1983) as has the H3 histone and a variant of H4 (T. Tabata, M. Iwabuchi, and M. Fukasawa, personal communication, 1984), and the genes for H2A, H2B and H1 are in the process of being sequenced (quoted in Tabata et al., 1983). It appears that these genes are not strongly clustered, in contrast to the situation in animal systems, and the ca. 100 copies of each gene are dispersed among a variety of other sequences. (The actual structure of these genes is discussed later.) Histones also may be modified through the addition of poly(ADP-ribose) by the enzyme

poly(ADP-ribose) polymerase (Laroche et al., 1980; Whitby et al., 1979; Sasaki and Sugita, 1982). Although it is known that this is a chromatin-bound enzyme that utilizes NAD^+ as one of its substrates, the function of the poly(ADP-ribose) additions to chromosomal proteins and the effects that these additions have on chromatin structure are presently unknown.

An important set of chromosomal proteins that have been studied in wheat are the RNA polymerases (Jendrisak, 1980). The availability of wheat embryos on a large scale has allowed the isolation of three protein complexes, RNA polymerase I (α-amanitin-insensitive transcription of rDNA), RNA polymerase II (α-amanitin-sensitive transcription of most genes), and RNA polymerase III (moderately α-amanitin-sensitive transcription of 5S and tRNA genes). These proteins show numerous low-molecular-weight units as well as the major subunit structures with molecular weights of 100 to 200 kd, analogous to those of other organisms.

A final set of proteins we can mention in this section are the high-mobility group (HMG) proteins (Fig. 5B–1); characteristically highly charged and low in molecular weight (Spiker, 1984a). The four HMG proteins isolated from wheat, a, b, c, and d, have molecular weights of 24 300, 20 400, 17 400, and 14 500kd, respectively, and the HMGb, HMGc, and HMGd proteins contain approximately 20 mol% of basic amino acids and 23 to 29 mol% of Asx and Glx residues (Spiker et al., 1978; Spiker, 1984b). The HMGa protein, however, is low in Asx and Glx (12 mol%) but does have the high proline content (13 mol%) that is associated with HMG proteins (Spiker, 1984a). In DNAase I digestion experiments of the type described above, the HMG proteins are lost from nuclei, which is consistent with the concept that HMG proteins are associated with transcriptionally active regions of the chromatin complex.

5B–1.2 Meiotic Chromosomes

A further aspect of the organization of chromosomes within nuclei is observed in the analysis of meiosis. Ultrastructural studies of wheat meiotic nuclei have revealed an interesting complexity with respect to interlocking of chromosomes which may be related to the arrangement of chromosomes within meiotic prophase nuclei. The reconstruction work of Hobolth (1981) and Jenkins (1983) suggests that in early meiotic prophase, chromosome pairing is not strictly homologous and can lead to interlocking which is subsequently resolved as the prophase progresses into pachytene. These studies have developed a new concept for the action of the *Ph1* mutant of wheat (Sears, 1977); namely, that it controls the time of crossing-over within meiosis rather than the actual alignment of chromosomes (Avivi and Feldman, 1980). Thus, in the absence of *Ph1*, crossing-over occurs when the nonhomologous associations seen in the earlier stages of prophase are not yet resolved. Necessarily, these observations are based on the reconstruction of small numbers of nuclei. Meiotic chromosome spreading techniques currently being developed for plants

(Fig. 5B–2; Gillies, 1981; Stack, 1982; Albini et al., 1984) will, it is hoped, provide new information on both the frequency and timing within meiosis of nonhomologous pairing. Currently, these techniques allow the synaptonemal complex (SC) component of paired meiotic chromosomes to be visualized in large numbers of nuclei. Details such as quadrivalent formation and heterozygosity of SC length can be assayed at the electron microscopic level (Fig. 5B–2), and further work should provide increased detail on the overall organization of meiotic nuclei.

5B–2 THE CLASSIFICATION OF DNA SEQUENCES

Considering the large amount of DNA in a wheat nucleus, it has proved useful to classify the DNA present into various categories of sequences based on their repetition frequency within the genome. The separation of the sequence classes relies on the observations by Britten and Kohne (1968) that denatured genomic DNA contains sequences that renature at different rates. At a given concentration of DNA, the rate of renaturation is dependent on the frequency of repetition of a particular DNA sequence; a sequence present in high frequency finds its complementary strands more readily and thus renatures faster than a sequence present in low frequency. A summary of technical and theoretical aspects of the determination of the renaturation characteristics of a DNA sample is given in Flavell (1982b) and renaturation curves for wheat DNA are shown in Fig. 5B–3. The data in the curves derive from the term C_0t, which is a function dependent on the concentration (C_0) of DNA in moles of nucleotides per liter multiplied by renaturation time (t) measured in seconds. To determine the fraction of DNA renatured at a given C_0t value, a number of different methods can be used (Flavell, 1982b). In large genomes such as wheat, very highly repeated sequences are considered to reanneal with a C_0t of < 0.01, repeated sequences with a C_0t of < 100, and low-copy and single-copy sequences with a $C_0t > 100$.

In wheat and its relatives, renaturation curves of the type shown in Fig. 5B–3 indicated that only 10 to 20% of the nuclear DNA belongs to the low-copy number category, while the bulk of the DNA (ca. 80%) is composed of repetitive sequences (Huguet and Jouanin, 1972a; Mitra and Bhatia, 1973; Flavell et al., 1974; Ranjekar et al., 1976, 1978; Flavell and Smith, 1976; Smith and Flavell, 1977; Flavell et al., 1977). A small fraction of the genome (4–10%) is composed of very rapidly reannealing sequences (Ranjekar et al., 1976, 1978; Flavell et al., 1977) which can be subdivided into two categories. One class consists of palindromic sequences, which form foldback intrastrand duplexes (Huguet et al., 1975; Bazetoux et al., 1978) in a fast reaction that does not involve any other single-stranded fragment of DNA. The other class consists of long tandem arrays (Appels et al., 1978; Dennis et al., 1980) and may also include sequences capable of forming foldback duplexes.

In addition to subdividing the genome on the basis of renaturation

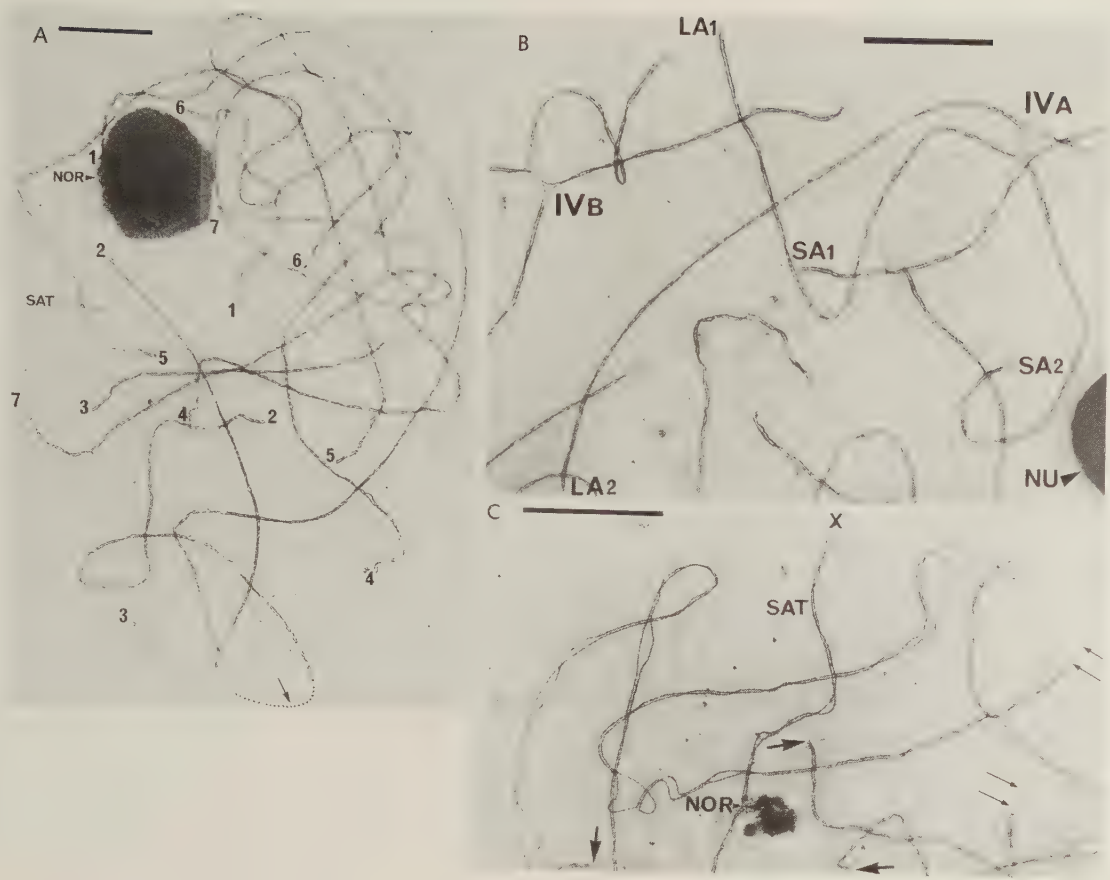
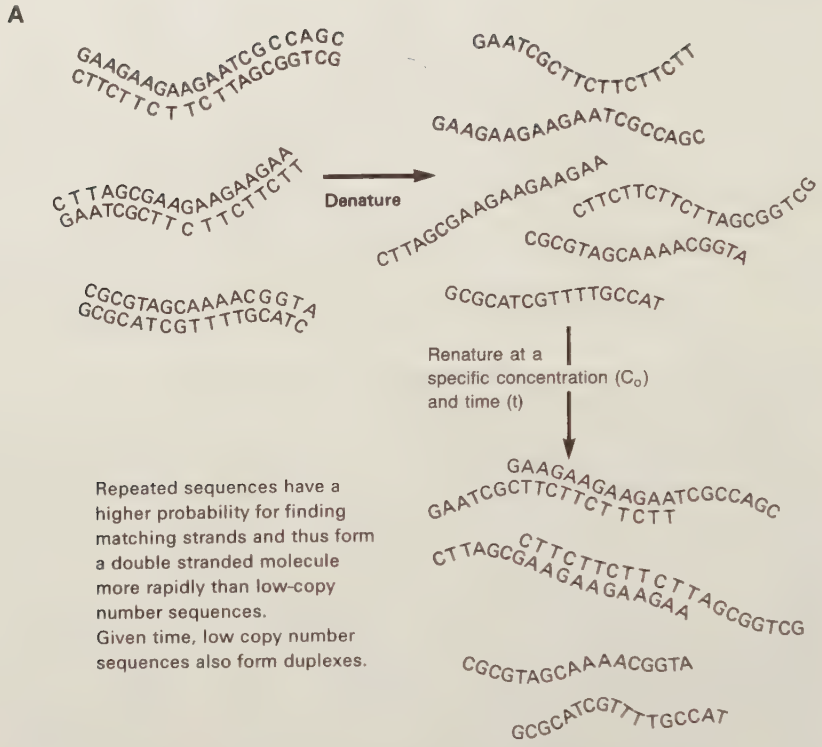


Fig. 5B–2. Synaptonemal complex spreading in cereals. These photographs were kindly supplied by C. B. Gillies.

A. The seven bivalent synaptonemal complexes from a pachytene nucleus of *T. monococcum*, numbered at each end from longest to shortest. Lengths range from 75.8 to 42.2 μm; the satellite is detached from the NOR. A portion of bivalent 2 has extended over the grid edge (arrow) and the part missing is shown by a dotted line drawn from light microscopy. $\times$4300 (bar = 5 μm).

B. Pachytene quadrivalent synaptonemal complexes from autotetraploid *T. monococcum*. Quadrivalent A. (IVA) is 16.4% of the complement length. The centromeres are at the interchange region, and the short (SA) and long (LA) arm telomeres are indicated. The interchange region of a second quadrivalent (IVB) is also shown. $\times$ 4500 (bar = 5 μm).

C. Rye (*S. cereale*) zygotene synaptonemal complexes with regions of unpaired lateral elements. Telomeric regions are fully paired (*large arrows*), unpaired (*x*), or have unequal lateral elements (*pairs of small arrows*). The NOR region and satellites (SAT) are indicated. $\times$ 4500 (bar = 5 μm).



B

Measuring the renaturation of denatured plant DNA yields a complex "C_0t" curve, reflecting the presence of different families of repetitive sequences.

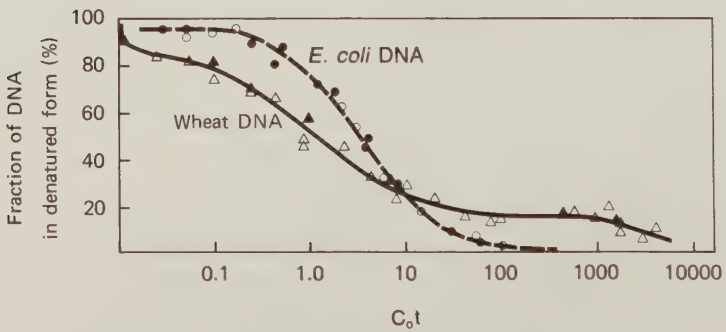


Fig. 5B–3. The renaturation of wheat DNA sequences.

A. Possible structures formed upon renaturation of a DNA sequence containing the GAA repeat sequence of wheat "silver" satellite, as well as unrelated sequences. We illustrate that renatured molecules usually have single-strand tails. With short renaturation periods, sequences present at a low frequency are also present as single strands.

B. A $C_o t$ curve for wheat DNA. The probability of complementary strands forming a duplex is related to the concentration of DNA (C_o) and time (t) allowed for renaturation. The product, $C_o t$, is used to plot curves of the type shown. The unimodal curve for *E. coli* (○ and ●) indicates that sequences in the bacterial genome are present only once or a few times. The multi-modal curve for wheat DNA (△, from Smith and Flavell, 1975, ▲, from Ranjekar et al., 1976) indicates the presence of highly repetitive DNA sequences (low $C_o t$ values), middle-repetitive sequences ($C_o t$ 0.1 to $C_o t$ 100), and low-copy-number sequences ($C_o t > 100$). The various methods for measuring the fraction of DNA in denatured form are summarized in Flavell (1982b).

analysis, buoyant density fractionation in cesium salts has been a valuable analytical tool. The buoyant density of DNA reflects its state of hydration and after high-speed centrifugation in a CsCl gradient, a band is formed where the density of CsCl is approximately 1.7 g mL^{-1}. The buoyant density of DNA also depends on its base composition, with A-T rich sequences having a lower density than G-C rich sequences. Differences in buoyant density can be further enhanced by the addition of small molecules which preferentially bind certain sequences (Kersten et al., 1966; Davidson et al., 1965). In wheat, this approach has been used to fractionate 5S RNA and rRNA genes from the bulk of the DNA (Hemleben and Grierson, 1978; Gerlach and Bedbrook, 1979; Gerlach and Dyer, 1980), the preference of the DNA-binding antibiotic actinomycin-D for G-C rich sequences being utilized. The preference of silver ions for A-T rich sequences has also been used to isolate long tandem arrays of repetitive sequences from wheat, rye, and barley, after banding to equilibrium in Cs_2SO_4 gradients (Huguet and Jouanin, 1972b; Ranjekar et al., 1978; Appels et al., 1978; Dennis et al., 1980).

Restriction enzymes provide another method of separating and classifying various classes of DNA sequence. The parameter utilized with this technique is the spacing of specific restriction-enzyme sites throughout the genome. Firstly, long tandem arrays of certain sequences may lack a restriction-enzyme site that is otherwise widely distributed in the genome: after restriction-endonuclease digestion, certain size classes of DNA are produced that can be isolated after electrophoretic separation. In the analysis of rye repetitive DNA, for example, a fraction of DNA with no recognition sites for the restriction enzyme HindIII was able to be purified from the bulk of the DNA. This fraction was shown to contain a major heterochromatic sequence of rye (Appels et al., 1981). Secondly, a repeated sequence may carry a regular restriction-enzyme site and when these sequences are digested, many DNA fragments of the same size are produced. After electrophoretic separation, these are visualized as numerous bands (Fig. 5B–4). The DNA fragments in a separation of this type can then be transferred from the separating gel to a solid matrix such as nitrocellulose or nylon filters (Southern, 1975), making the fragments available for hybridization with radioactive probes (see also Fig. 5B–5). In this way, specific sequences can be recognized within the DNA fragments by virtue of their complementarity to the radioactive probe. This technique is used extensively in conjunction with cloned DNA sequences (used as radioactively labeled or biotinylated probes) to map polymorphisms for restriction-enzyme sites near specific gene sequences. The polymorphisms can then be used in genetic studies, as is discussed below.

5B–3 DNA RELATIONSHIPS WITHIN THE TRITICEAE

Changes in chromosomal DNA content may well have taken place during the co-evolution of the A, B, and D genomes of hexaploid wheat.

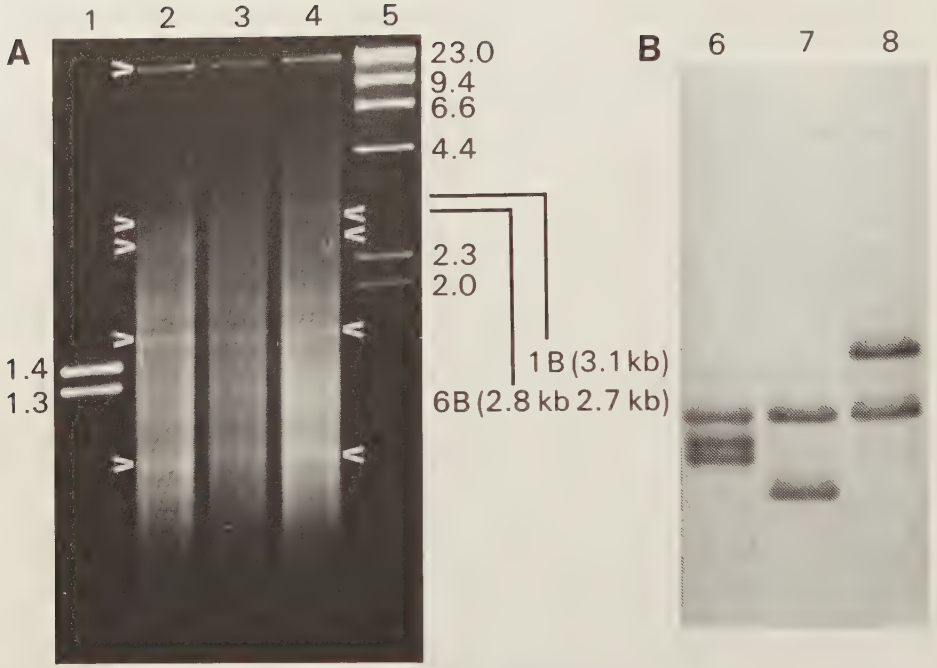


Fig. 5B–4. Restriction endonuclease digestion of wheat DNA.

A. The restriction endonuclease TaqI was used to digest samples of wheat DNA: 2,6—'Chinese Spring' (CS); 3,7—'Hope' 2B(CS2B); 4,8—'Timstein' 2B(CS2B). DNA fragments were separated by electrophoresis in a 1.2% agarose gel and visualized using the dye ethidium bromide and UV light. The arrows indicate families of repeated sequences which have TaqI digestion sites equally spaced so that the fragments appear as a band. Length markers are usually provided by digesting well-characterized bacterial DNAs such as the plasmid pBR322 (1), and bacteriophage λ (5), as shown.

B. Specific DNA sequences can be assayed in the electrophoretic separations by transferring the DNA to membranes after alkaline denaturation (Southern, 1975) and hybridizing to radioactively labeled DNA or RNA probes. The position of the sequence with which the probe hybridizes is established by exposing the treated membrane to x-ray film. In the example shown, TaqI digests of wheat (6, 7, 8) were hybridized with a ^{32}P-probe to assay the rDNA spacer region (see Fig. 5B–6). The assignment of bands to specific chromosomes is based on Appels and Dvořák (1982a). Note the extent of polymorphism in the lengths of the spacer region in the three cultivars. This is typical of species examined in the Triticeae (Dvořák et al., 1984b; Appels and Moran, 1984).

An indication of such comparatively gross changes is provided from measurements of the DNA content of nuclei and individual chromosomes. The latter were measured by Nishikawa and Furuta (1979) who showed that the DNA in the A, B, and D genome chromosomes of *T. aestivum* is present in a ratio of 1.14:1.2:1. This is in good agreement with the metaphase chromosome measurements of Sears (1954) and Dvořák et al. (1984c), in which the ratios were 1.08:1.24:1 and 1.15:1.38:1, respectively. Comparisons of these ratios with those obtained from the diploid species thought to contribute the respective genomes indicate some discrepancies (Rees and Walters, 1965; Bennett and Smith, 1976; Nishikawa and Furuta, 1979). *T. monococcum*, the species considered to be the A

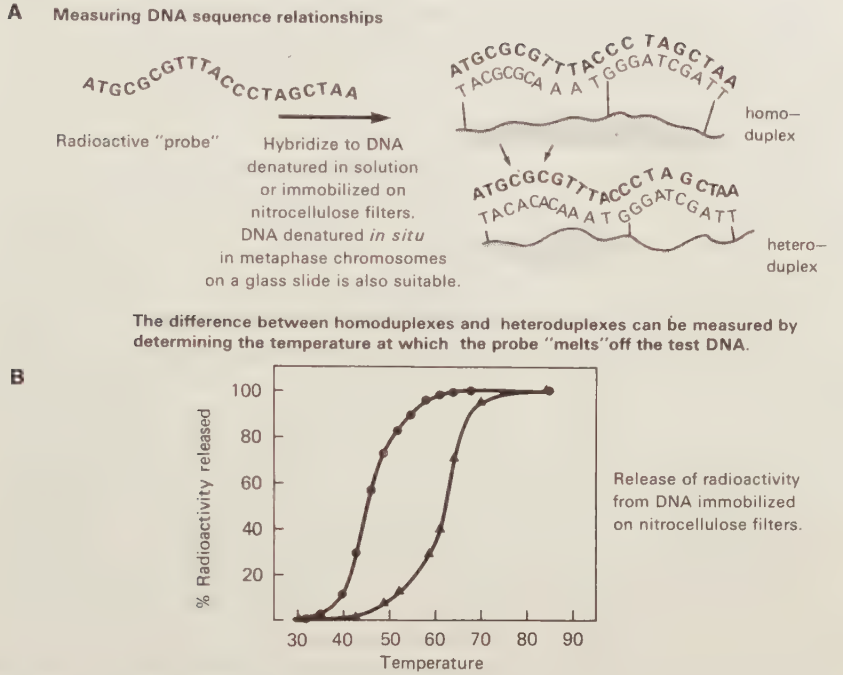

A
Measuring DNA sequence relationships
ATGCGCGTTTACCCTAGCTAA
Radioactive "probe"
Hybridize to DNA denatured in solution or immobilized on nitrocellulose filters. DNA denatured in situ in metaphase chromosomes on a glass slide is also suitable.
ATGCGCGTTTACCC TAGCTAA
TACGCGCA A A TGGGATCGATT
homo–duplex
ATGCGCGTTTACCCTA GCTAA
TACACACAA A TGGGATCGATT
hetero–duplex
The difference between homoduplexes and heteroduplexes can be measured by determining the temperature at which the probe "melts" off the test DNA.
B
% Radioactivity released
100
80
60
40
20
30 40 50 60 70 80 90
Temperature
Release of radioactivity from DNA immobilized on nitrocellulose filters.

Fig. 5B–5. Measuring DNA sequence relationships.
A. Diagrammatic representation of the pairing of a single-stranded radioactive probe to form a homoduplex or heteroduplex (arrows indicate positions of base pair mismatch).
B. A radioactive probe of the 134 bp spacer sequence in wheat rDNA (see Fig. 5B–6) was hybridized to wheat to form a homoduplex (▲) and to rye DNA to form a heteroduplex (●). The difference in melting points of the hybrids ($\Delta Tm = 14°C$) indicates at least a 17% mismatch.

genome donor, tends to have more DNA than the A genome in hexaploid wheat, while *T. tauschii* tends to have less DNA than is contained in the D genome chromosomes. These differences suggest an amplification or diminution of chromosomal DNA during the period of co-evolution (Mitra and Bhatia, 1973; Flavell, 1982a); the mechanisms involved probably include chromosomal translocations and substitutions, as well as changes at a molecular level resulting from processes such as unequal crossing over.

At the DNA level, interspecific relationships within the Triticeae have been investigated in two types of experiment. The first we shall discuss uses a radioactively labeled, heterogeneous DNA probe from one species which is mixed with a large excess of DNA from another species and allowed to hybridize in solution (Fig. 5B–3). In the second type, a particular cloned DNA segment from one species provides the labeled probe and this is hybridized to an excess of DNA from another species, immobilized on a solid matrix such as a nitrocellulose filter. In both types of experiment, the degree of base pair matching between the labeled probe and the unlabeled DNA is assessed by increasing the temperature of the

DNA-DNA hybrids and determining the T_m of the matched strands. T_m is the temperature at which 50% of the DNA-DNA hybrids are dissociated (Fig 5B–5). The radioactive probe renatured to itself provides a reference T_m and denotes the value expected for the best possible base pair matching. Mismatching between the radioactive probe and the test DNA is indicated by a lowering of the T_m of the heteroduplex relative to the reference T_m of the homoduplex and is designated the ΔT_m. A ΔT_m of 1°C corresponds to an average of 1.2 to 1.5% mismatch of base pairs in the hybrids analysed (Laird et al., 1969; Appels and Dvořák, 1982a).

The first type of experiment has been performed in a number of laboratories (Bendich and McCarthy, 1970a, 1970b; Mitra and Bhatia, 1973; Flavell et al., 1979; Nath et al., 1983, 1984). Generally, the DNA of one species is radioactively labeled by growing seedlings in a solution of tritiated thymidine. The DNA is then extracted and sheared by sonication to a size of 300 to 500 bp. This labeled DNA is then mixed with a 100 to 1000-fold excess of sheared, unlabeled DNA from another species, the excess of unlabeled DNA ensuring that the labeled DNA can form heteroduplexes only. The mixture is then denatured by heat or alkali and is incubated to a desired $C_o t$ value. The double-stranded and single-stranded fractions of DNA are then separated from each other by hydroxylapatite chromatography or S1 nuclease treatment (Fig. 5B–3; Flavell et al., 1979). The degree of base-pair matching between the labeled and unlabeled DNAs is assessed by determining the temperature needed to separate the strands (Fig. 5B–5). The DNA analyses that have been described are generally in agreement with the evolution of hexaploid wheat as determined by cytogenetic analyses (e. g., Kimber and Sears, this chapter).

The second experimental approach to examining relationships among the Triticeae uses specific or cloned probes. We illustrate this type of analysis using the rDNA loci of wheat as an example. The structural information available for these loci is summarized in Fig. 5B–6. The 132 to 134 bp repeat sequence in the spacer region has been shown to be evolving rapidly (Appels and Dvořák, 1982b; for a recent review, see Appels and Honeycutt, 1986) and sequence differences within the spacer regions can, therefore, be used to determine relationships among the Triticeae. Although such relationships refer strictly to the rDNA loci, they correlate reasonably well with analyses of the type described earlier and with other classical taxonomic parameters. The rankings, as shown in Fig. 5B–7, are relative to *T. aestivum* cv. Chinese Spring and are based on T_m differences. An interesting feature is that, of the S-genome related diploids, the rDNA loci of *T. speltoides* are the most closely related to those of *T. aestivum*. This contrasts with cytogenetic and DNA renaturation analyses (e. g., Shands and Kimber, 1973; Nath et al., 1984b) and serves as a further reminder that the genomes of hexaploid wheat are most likely a mixture of genomes as defined by present-day diploid species.

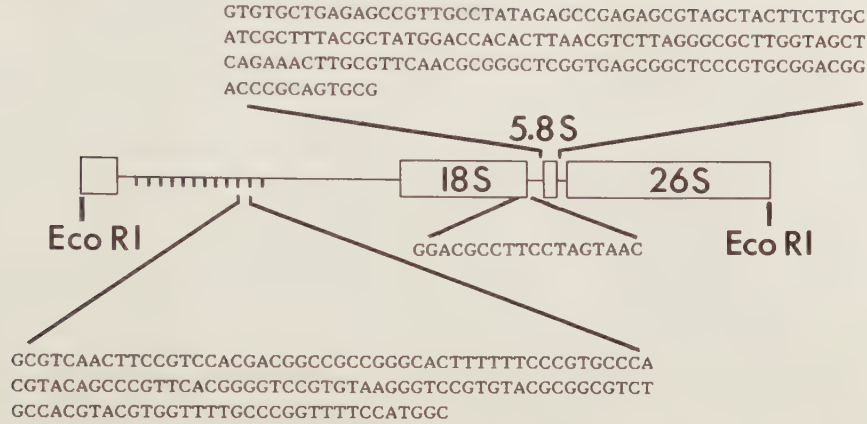


Fig. 5B–6. Structure of wheat rDNA.
The repeat unit of wheat rDNA is defined by a single site for the restriction endonuclease EcoRI (Gerlach and Bedbrook, 1979). The order of the RNA components was determined by Appels et al. (1980) and the nucleotide sequence of a 134 bp repeat unit from the spacer DNA is from Appels and Dvořák (1982a). The 3′ end of the 18S rRNA gene is from Hagenbuchle et al. (1978) and the 5.8S rRNA gene sequence from Mackay et al. (1980). The EcoRI units were cloned in the vector pACYC184. The chromosomal locations of the rDNA genes are shown in Fig. 5B–8C.

The length of the rDNA spacer sequence is also a highly variable character (Fig. 5B–4), although within a given locus the 1000 to 3000 rDNA units that are present tend to be homogeneous (Appels and Dvořák, 1982a). Particular length variants present on chromosomes 1B and 6B of *T. aestivum* have been found in natural populations of *T. speltoides*. There can also be large quantitative changes in the numbers of rDNA genes: in *T. tauschii*, for example, some 5 700 rDNA genes are present (Liang et al., 1978) whereas in *T. aestivum* the D genome accounts for only 130 to 400 rDNA genes (Flavell and O'Dell, 1976; Appels et al., 1980). As is the case for the B genome, the spacer length assigned to chromosome 5D in *T. aestivum* can be found in natural populations of *T. tauschii* (Appels and Dvořák, 1982a) and it is possible that accessions of this diploid with differing numbers of rDNA genes may yet be found. When variations in unit length are combined with sequence data and numbers, it may eventually prove possible to be quite precise as to the origin of specific chromosomes in hexaploid wheat.

5B–4 DNA SEQUENCES FOR DETECTING SPECIFIC CHROMOSOME SEGMENTS

Early analyses of DNA renaturation in cereals provided the first indications about the overall organization of the cereal genome. These studies utilized the cross-reaction between DNA molecules from wheat, rye, barley, and oats, and provided evidence for extensive interspersion

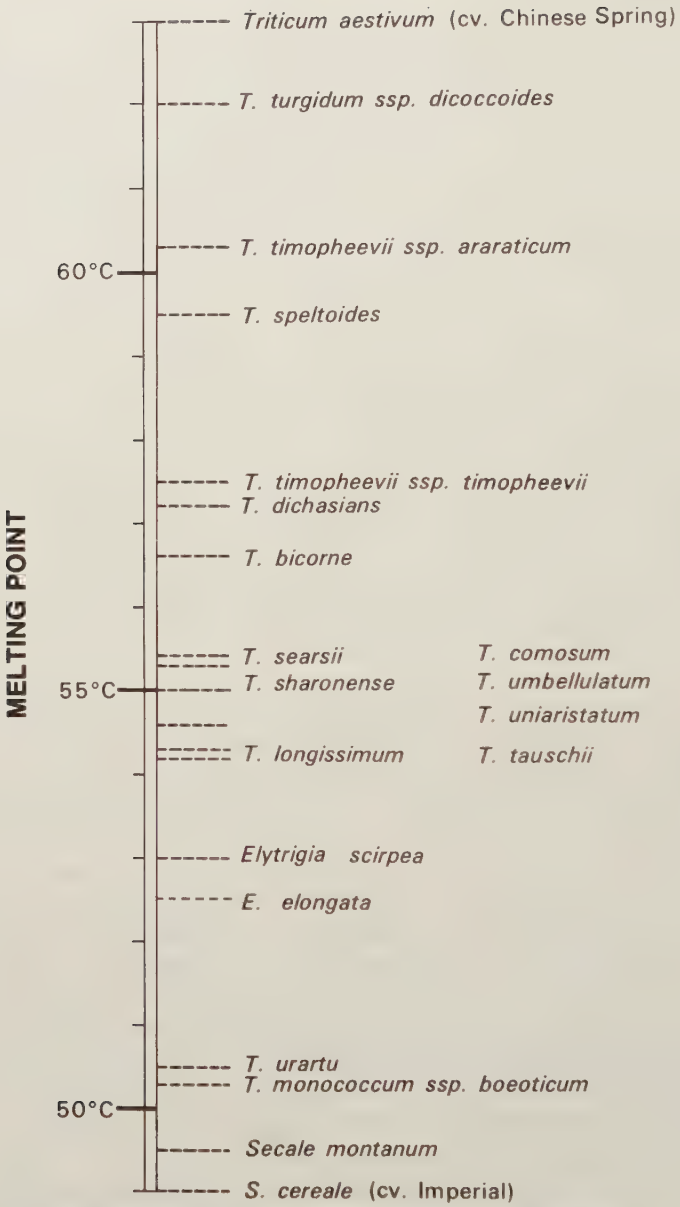


Fig. 5B–7. Sequence changes in the rDNA spacer regions of the Triticeae.
The rankings reflect changes in T_m relative to *T. aestivum* using the 134 bp sequence from hexaploid wheat (Fig. 5B–6). The melting-point determinations were carried out as illustrated in Fig. 5B–5 and were originally determined by Dvořák and Appels (1982).

of various classes of repetitive DNA sequences among each other as well as among so-called nonrepeated DNA sequences (Flavell et al., 1977; Rimpau et al., 1978). Regions in which nonrepeated DNA sequences were free of repetitive DNA sequences were also detected. An important finding was that in comparing wheat and rye DNAs, some repetitive DNA sequences dispersed among nonrepeated DNA sequences were also specific to wheat or rye. Analogous, apparently species-specific repetitive sequences have also been assayed among diploid *Triticum* spp. (Flavell et al., 1979) and the occurrence of sequences of this type may well be a general phenomenon. Using in situ hybridization, Appels et al. (1978) have shown that some tandem arrays of repetitive DNA sequences in rye are virtually absent from wheat and can be defined as rye-specific. The discovery of these apparently recently evolved sequences has opened up a new area of research in cereal DNA analysis.

The first example of an analysis of a specific chromosome region is found in studies of the rDNA loci. Initially, this was possible using in vivo labeled ^{3}H-rDNA (Flavell and O'Dell, 1976) or chemically iodinated ^{125}I-rRNA (Appels et al., 1980). These studies established the location of the rDNA genes on chromosomes 1B, 6B, and 5D of *T. aestivum* cv. Chinese Spring (e. g. Fig. 5B–8C) and provided evidence for marked variation in the number of genes at each locus. Depending on the other cultivars analysed, the number of rRNA genes on chromosome 1B ranges from 1300 to 1500; on 6B, from 500 to 3000; and on 5D, from 130 to 400 (Flavell and Smith, 1974a; Flavell and O'Dell, 1976; Appels et al., 1980). Although there are no detectable rDNA units on chromosome 1A of Chinese Spring wheat (Appels et al., 1980), *T. aestivum* ssp. *spelta* has a major location for rDNA (approximately 2500 units) on this chromosome (Flavell and Smith, 1974b; Miller et al., 1980), as have the AA genome diploid wheats (Gerlach et al., 1980). An rDNA locus on chromosome 5A of AA diploid wheats is also found in the hexaploid *T. zhukovskyi* (Hutchinson and Miller, 1982) but in no other polyploid wheat (Miller et al., 1983). Tetraploid wheats have their major rDNA loci on chromosomes 1B and 6B (Dvořák and Appels, 1982) as do diploids in the Sitopsis section (Miller et al., 1983; Dvořák et al., 1984b), and the numbers of rDNA units are in similar proportions to those of *T. aestivum* cv. Chinese Spring (Carrozza, 1981; Hutchinson and Miller, 1982; Teoh et al., 1983a). Other relatives of wheat have been investigated using wheat rDNA probes and major rDNA loci have been found on chromosomes 1R of rye (*Secale cereale*), 6 and 7 of barley (*Hordeum vulgare*), and 5E and 6E of wheat grass, *Elytrigia elongata* (Appels et al., 1980; Miller et al., 1983; Appels and Moran, 1984; Dvořák et al., 1984b).

Using purified rRNA as a probe, the detailed structure of the rDNA genes could be assayed using electron microscopy and the R-loop technique, and by mapping the location of restriction-endonuclease sites within the gene unit (Appels et al., 1980). Cloning of the basic rDNA unit by

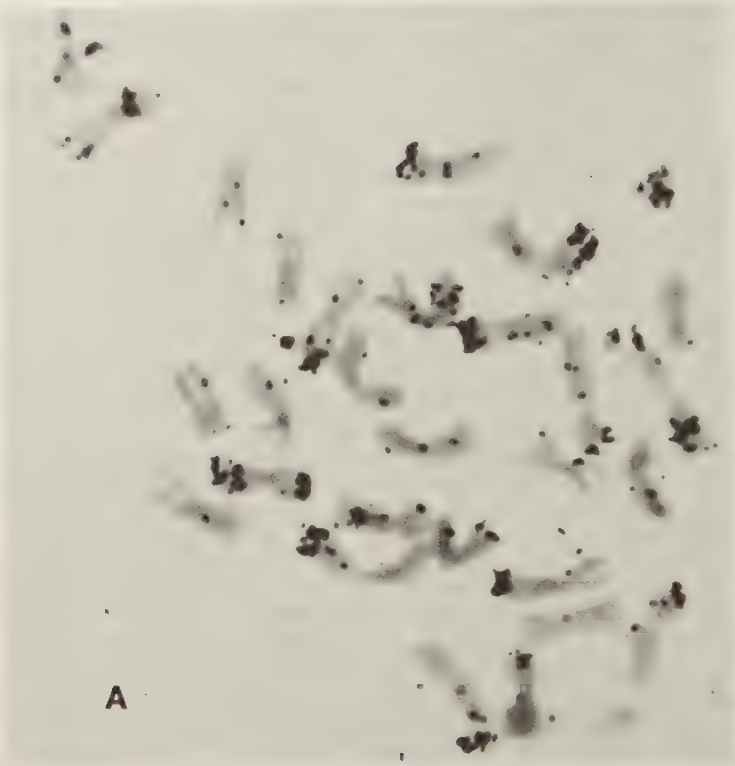


Fig. 5B–8. In situ hybridization using specific DNA probes. The molecular probes were synthesized from DNA templates using RNA polymerase from *E. coli* and ^{3}H-labeled nucleotide precursors. The four probes illustrated were hybridized in situ to metaphase chromosomes from root-tip cells.

Fig. 5B–8 *A*. Distribution of a wheat sequence cloned in the plasmid pCSC40 (Hutchinson and Lonsdale, 1982) and applied to 'Chinese Spring'. Note that very little of this sequence is located near the centromeres. Photograph kindly supplied by J. Hutchinson-Brace.

Gerlach and Bedbrook (1979) allowed a more detailed analysis of the 9.5 kb repeat sequence (Appels and Dvořák, 1982a) and a map of the DNA sequence is shown in Fig. 5B–6. As we have noted previously, the spacer region of the rDNA unit is a good example of a DNA sequence that is evolving at a rate fast enough to provide genus-specific probes. This was further demonstrated by Appels and Moran (1984) who used the spacer region from pHv132—a barley rDNA clone isolated by Gerlach and Bedbrook (1979)—to specifically assay for barley chromosomes 6 and 7 in disomic addition lines of barley chromosomes to wheat (Islam et al., 1981).

The 5S RNA of wheat (chemically labeled with ^{125}I) has also been used to assay for the respective loci on 1R of rye and 1B of wheat. In both cases, the 5S genes were located distal to the secondary constriction (Appels et al., 1980): the genes assayed in barley were not assigned to particular chromosomes. In wheat, there are other minor sites for the 5S

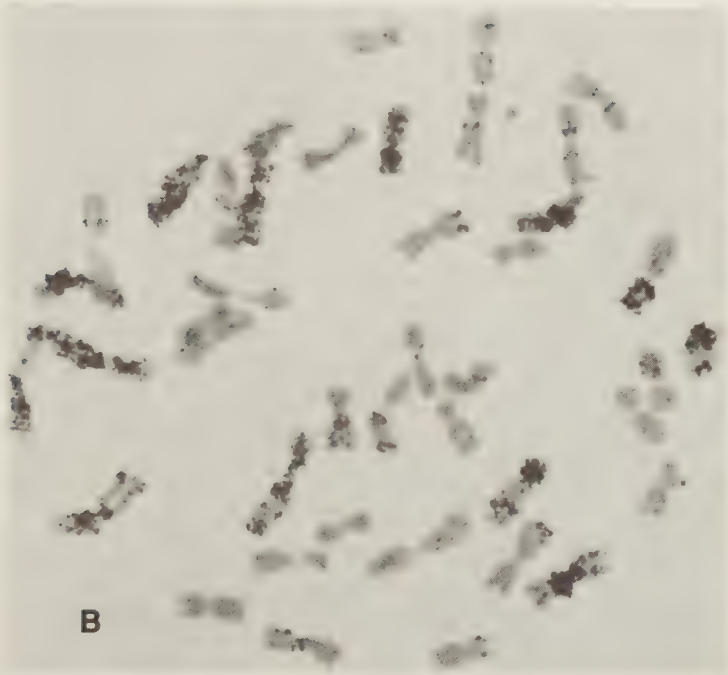


Fig. 5B–8 *B*. Distribution of the wheat "silver" satellite sequence assayed using the DNA sequence $(GAAAGA)_n$, $(GAAGAGA)_n$ (May and Appels, 1980). In contrast to the sequence in pCSC40, many centromeres are heavily labeled by this probe. The plant shown had its 2B chromosomes substituted by chromosome 2R of rye and a 2BS/2RL translocation. Some of the sequences in the wheat "silver" satellite have been cloned and are largely comprised of GAA and GGA sequences (Peacock et al., 1981; Gerlach et al., 1983).

genes on 1D, 5A, 5B, and 5D; the 5S DNA unit of the group 1 chromosomes is 410 bp long while the group 5 homoeologues have a unit that is 500 bp long (Appels et al., 1980; J. Dvořák and M. Lassner, personal communication, 1984). Examples of both the short and long 5S DNA units have been sequenced (Gerlach and Dyer, 1980) and again, it is likely that probes derived from the spacer regions of these units will be useful as probes for specific chromosomes.

Using chromosomal in situ hybridization (Appels et al., 1978), and filter hybridization (Flavell et al., 1978), the tandem arrays of repetitive sequences located in rye heterochromatin were found to be valuable markers for rye chromosomes after these had been introduced into wheat. The cloning of rye sequences from this heterogeneous group of sequences was achieved using the plasmid vectors pBR322 (Bedbrook et al., 1980) and pBR325 (Appels et al., 1981). The DNA sequences from the 480, 610, and 630 bp families (as defined by Bedbrook et al., 1980) and the major heterochromatic sequence family as represented by pSc7235 (Appels et al., 1981) are of particular interest. These define families of tandemly repeated sequences found in rye but virtually absent from wheat. The "480bp" and the "major heterochromatic sequence" belong to the

Fig. 5B–8 *C*. The 134 bp spacer sequence of rDNA (see Fig. 5B–6) used to assay for the rDNA loci in an F_1 plant of a cross between double ditelo 1A 'Chinese Spring' and 'Cheyenne' (Appels and Dvořák, 1982a). The major locations of the rDNA units are on the short arms of 1B and 6B, some two-thirds of the length of the arms from the centromere. On the other hand, genetic linkage studies on both of these chromosomes indicate little recombination between the centromere and the rDNA loci. Genetic distances to seed storage-protein genes have been determined (Dvořák and Chen, 1984; Payne et al., 1984a).

same family and are composed of tandemly repeated units 379 bp in length; this sequence is referred to as the 350 family (Appels, 1983). This probe has been used to characterize triticales (Fig. 5B–8D; Appels et al., 1982; Jones and Flavell, 1982a; Appels, 1983), to determine the rye chromosomes present in triticale × wheat hybrids (May and Appels, 1982), and to provide a parameter for the registration of new cultivars of Australian triticales. The probe has also been used to identify the translocation chromosome 2RS/2BL in wheat backgrounds which, in certain situations, involved this chromosome with seedling lethality (May and Appels, 1984). The rye sequences cloned by Bedbrook et al. (1980) have been characterised with respect to their chromosomal distribution in species of *Secale* (Hutchinson et al., 1981; Jones and Flavell, 1982a, 1982b). Large quantitative changes in the content of these sequences are evident within the genus which is consistent with the view that these sequences are of recent origin (Appels, 1983). However, the 120 bp family of sequences is also present in species of *Haynaldia*, *Hystrix*, *Elytrigia*, and *Elymus*, and labels 7 of the 14 pairs of chromosomes of *T. turgidum* (Hutchinson et al., 1981). Given the latter, it is perhaps not coincidental that this sequence labels the seven pairs of chromosomes of *T. speltoides* (Jones, 1981 quoted in Flavell, 1982a). Clearly, this may well be a useful probe to further elucidate genomic relationships in the Triticeae.

The DNA of *Elytrigia elongata* (Host) Nevski and *Haynaldia villosa* (L.) Schur. has been analyzed to find repetitive sequences that could be cloned and used to follow the chromosomes of these species as they are introduced into wheat (Appels and Moran, 1984). The cloning scheme used was based on bacteriophage λ and is outlined in Fig. 5B–10. The sequences recovered appear to be of the dispersed repetitive type and were of use in detecting the alien chromosomes in the lines that were then available. A major dispersed repetitive sequence from rye, the 5.3 sequence, has also been recovered using λ cloning (Appels and Moran, 1984) and this sequence has been shown to specifically assay rye chromosomes in the respective addition lines (Appels and Moran, 1984) and in triticales (May and Appels, unpublished). From these examples, it seems likely that an extensive set of DNA probes could be manufactured from dispersed repetitive sequences and used to detect a wide gamut of alien chromosome segments after these have been introduced into wheat.

It is not only in the detection of alien chromosomes that molecular probes are of use. A number of clones from the wheat genome itself have been isolated and used to identify the chromosomes of wheat. Many of these probes are not necessarily specific to wheat, although such classes of sequence are numerous and readily isolated when appropriate screening procedures are carried out (Appels and Moran, 1984; R. Appels, unpublished observations). The first indication that useful wheat sequences could be present came when a heterogeneous, highly repetitive fraction of wheat DNA was used as a probe and found to predominantly label the B genome chromosomes (Gerlach and Peacock, 1980). More detailed

Fig. 5B–8 *D.* Distribution of a major heterochromatic sequence of rye applied to the triticale TNT6 (May 1983) showing labeling of all seven pairs of rye chromosomes. This 350 family probe has been cloned and sequenced (Appels et al., 1981; Appels and Moran, 1984). The consensus sequence for this family is 379 bp long, as derived from the sequencing of 16 of the repeat units, and is shown in the lower part of the photograph. A probe for rye heterochromatic sequences has also been used in a protocol combining in situ hybridization and C-banding (Hutchinson and Seal, 1983).

studies were then carried out on a subfraction of this DNA, isolated as a satellite DNA in buoyant density gradients of cesium sulfate containing silver ions. The very simple, tandemly repeated sequence present in this "silver" satellite of wheat (Gerlach et al., 1979; Dennis et al., 1980) has been cloned and sequenced (Peacock et al., 1981; Gerlach et al., 1983), although the sequence seems to be unstable in the cloning vectors used (W. L. Gerlach, personal communication, 1984). It is of interest, however, that stable insertions of the sequence, $(GAAGA)_n$, have been obtained from *Drosophila melanogaster* (A. Lohe and D. Brutlag, unpublished observation). This *D. melanogaster* sequence has been used to assay the regions of the wheat genome containing "silver" satellite DNA (Fig. 5B–8B; May and Appels, 1980) and is satisfactory for the routine monitoring of the seven pairs of B genome chromosomes as well as chromosomes 4A and 7A. In rye, there are two interstitial sites (Appels et al., 1978) and in barley, all the centromeric regions show this sequence (Dennis et al., 1980).

A number of other repetitive sequences from wheat (pTA8, pCSC40, and pCSTC22b), have been isolated and used to study *Triticum* chromosomes (Flavell et al., 1980; Hutchinson et al., 1980, 1981; Hutchinson and Lonsdale, 1982) (Fig. 5B–8A). In some cases, as with the rye heterochromatic sequences, the DNA probes detect chromosome regions assayed by various cytochemical techniques. In other instances, molecular probes provide a specificity and/or reproducibility that is otherwise lacking; this was used to advantage by Miller et al. (1982a) in the identification of a group 4 homoeologue from *T. longissimum.*

Analyses at the DNA level using restriction-enzyme digestion are also capable of detecting specific DNA sequences; consequently, length polymorphisms of particular DNA segments can be found. These may mark specific chromosomes. One approach to isolating new markers from specific chromosomes is discussed in Fig. 5B–9. The scheme is hypothetical but serves to show that the approach is applicable to investigations of the different genomes of wheat and to the identification of alien chromosome segments introduced into wheat. We note that, although the existence of repetitive sequences specific to the D genome has not been directly demonstrated (Flavell et al., 1979), their presence can be implied from variations found in the rDNA loci; these indicated that the rDNA spacer region of *T. tauschii* is highly diverged from those of chromosomes 1B and 6B (Dvořák and Appels, 1982). Clearly, other specific sequences will be found. A second approach to the isolation of specific DNA markers is to prepare a set of DNA clones (see Fig. 5B–10) and screen these for polymorphic markers (Burr et al., 1983). Recovery of a useful marker can then be followed up by chromosome mapping, using the cytogenetic stocks available in wheat, and by genetic linkage to known markers. The rDNA spacer polymorphisms described by Appels and Dvořák (1982a) have already provided a basis for a study of the genetic linkage to gliadins (Dvořák and Chen, 1984). It is clear that in years to come, many new

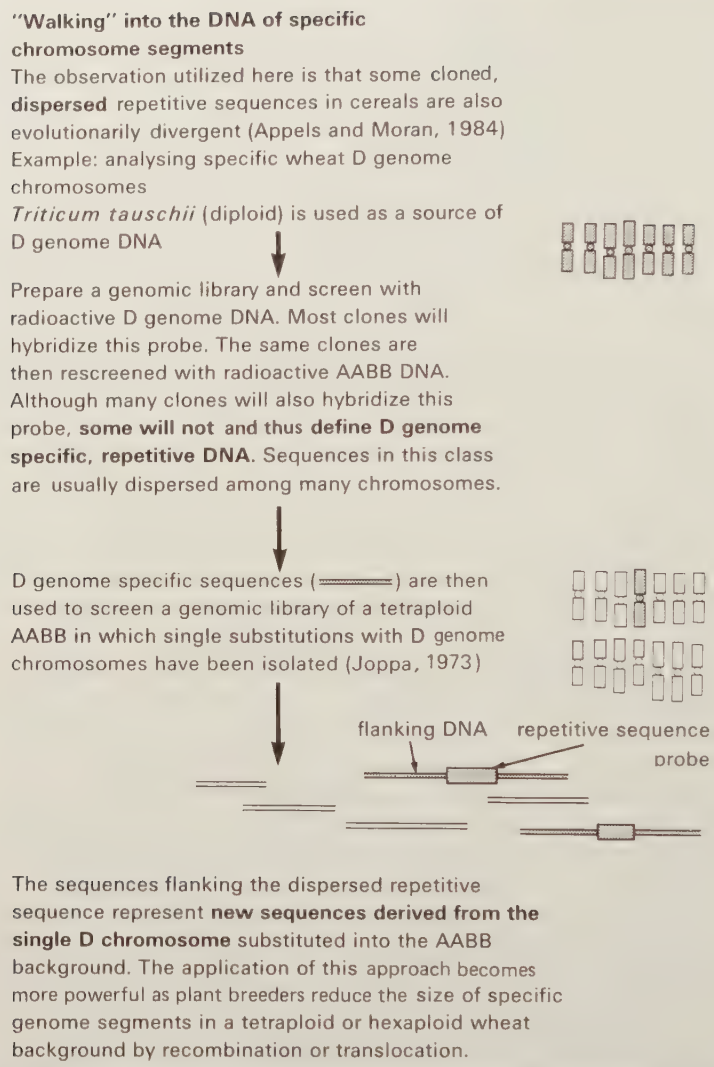

"Walking" into the DNA of specific chromosome segments
The observation utilized here is that some cloned, dispersed repetitive sequences in cereals are also evolutionarily divergent (Appels and Moran, 1984)
Example: analysing specific wheat D genome chromosomes
Triticum tauschii (diploid) is used as a source of D genome DNA
Prepare a genomic library and screen with radioactive D genome DNA. Most clones will hybridize this probe. The same clones are then rescreened with radioactive AABB DNA. Although many clones will also hybridize this probe, some will not and thus define D genome specific, repetitive DNA. Sequences in this class are usually dispersed among many chromosomes.
D genome specific sequences (═══) are then used to screen a genomic library of a tetraploid AABB in which single substitutions with D genome chromosomes have been isolated (Joppa, 1973)
flanking DNA
repetitive sequence probe
The sequences flanking the dispersed repetitive sequence represent new sequences derived from the single D chromosome substituted into the AABB background. The application of this approach becomes more powerful as plant breeders reduce the size of specific genome segments in a tetraploid or hexaploid wheat background by recombination or translocation.

Fig. 5B–9. A protocol for "walking" into the DNA of specific chromosomes. An analysis of the D genome of wheat is exampled.

DNA markers will be found, their positions on cereal chromosomes will be mapped, and they will then be used to extract adjacent DNA sequences, as we discuss below.

5B–5 THE STRUCTURE OF GENES AND THEIR IMMEDIATE ENVIRONMENT

At the time of writing, only a few genes of wheat and its relatives have been cloned and characterized. It is apparent, however, that several

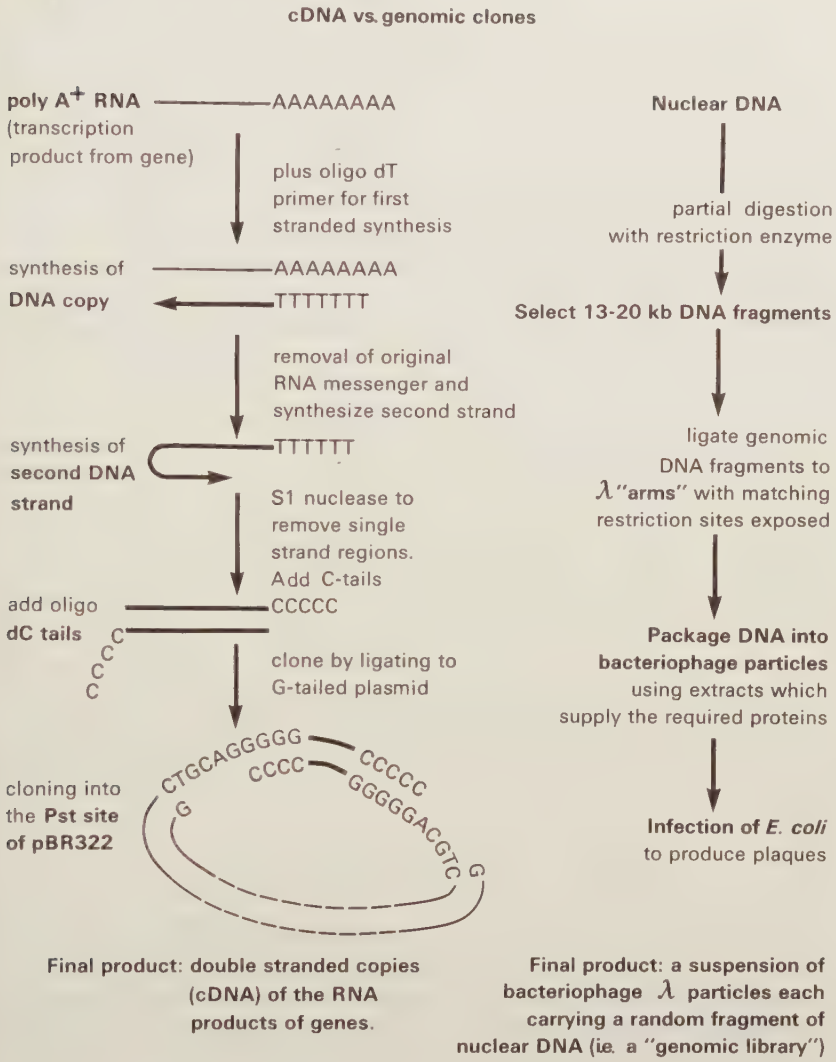


Fig. 5B–10. A comparison of cDNA and genomic cloning procedures.

of the features first discovered in animal genes are also found in the genes of cereals. The structures of some 20 plant genes have been reviewed by Messing et al. (1983) and, following their general outline, we will describe the structure of the wheat genes characterized to date.

5B–5.1 Intervening Sequences

The term *intervening sequence* or *intron* describes a noncoding DNA segment which occurs as an interruption in the DNA structure of a gene. The only wheat gene that has so far been found to contain an intervening

sequence is the gene for the small subunit of ribulose-1,5-bisphosphate carboxylase, or rubisco (Broglie et al., 1983). The single intron of this gene is 289 bp long and separates the transit peptide from the main portion of the protein (Fig. 5B–11). The position of the intron was determined by comparing cDNA clones with genomic clones (see Fig. 5B–10) and it was found that the first and last two base pairs were $\frac{GT}{CA}$ and $\frac{AG}{TC}$, respectively. This observation has been made in every eukaryote gene (coding for a protein) examined and suggests a highly conserved mechanism for splicing out the intron from the messenger-RNA transcript of the gene to produce the final template for translation (Messing et al., 1983). Other wheat genes that have been characterized in sufficient detail to determine the presence or absence of introns are a gliadin class I protein gene (Rafalski et al., 1984), the gene for gliadin α–1Y (Anderson et al., 1984), and histones H3, H4, and H4-variant (Tabata et al., 1983; T. Tabata, M. Iwabuchi, and M. Fukasawa, personal communication, 1984). No introns have been found in these genes. The lack of introns in the histones is not surprising since no introns have ever been found in these genes, whether extracted from plants or animals.

Sequencing of the 5S RNA genes of wheat revealed a 15 bp duplication in the middle of one of the genes (Gerlach and Dyer, 1980). It was argued that this leads to inactivation of the gene which would be analogous to the situation found in *Drosophila*. Alternatively, the 15 bp duplication could be a form of intervening sequence even though it is not bounded by the characteristic base pairs. It is emphasized, however, that these are only indicative of the introns of genes that produce proteins (reviewed in Cech, 1983) and are not applicable to ribosomal or tRNA genes.

5B–5.2 Initiation of Transcription

There are two aspects that relate to the initiation of transcription of a gene. The first is the position at which RNA polymerase molecules start transcription; this is usually at a specific DNA sequence. The second relates to control sequences that modulate transcription in an ON/OFF fashion or that modulate the frequency of transcription in response to certain environmental signals. Genes that utilize RNA polymerase II (i.e., all of those that eventually code for proteins) have a characteristic region containing only A and T residues 28 to 36 bp before, or upstream from, the actual starting point of transcription. This is the so-called TATA box that is apparently required for correct binding and positioning of RNA polymerase II molecules. In the wheat genes that have been examined, this region has the structures seen in Table 5B–2. The sequence of the 5S rDNA gene units determined by Gerlach and Dyer (1980) also defines the point of transcription initiation of these genes. These authors noted the sequence $\frac{ATAAG}{TATTC}$ at positions -29 to -25, which is identical to the sequence found at an analogous position in *Drosophila 5S* rRNA genes. It is thus possible that this sequence is important for RNA polymerase

```
                                    BamHI
-653                          5'...GATCCGGTGACTCAAAAAAGAAGAGCCGCCATCTG

-618     TCCAAGCGCCACTCCTACGAGAACTAAAATCCTATTCCCTCCGTAAATAAATATAAGAGT

-558     GTTTAGATCACTACTTCTTTACAGAGAATTTCCTTCCCTCCAAGGGGAGGCGAATCCATA

-498     GGCACATCGACGGATATGGAGGGGGGAAACATATATTTTACTATGCTAGTTCAGTTAATT

-438     CTACCAAGAAAACATATATTTTATTTTGACAAACATTGTATAAATGTAGACATTCACATA

-378     CACGTATGTACACCACCCTCTATGATTGCACACCCGCACACTATATGCCTATGAGCATAC

-318     TTTCAAGAGTGAGCCAGCAAATTTTATGATAAAATGAAATATTTTGCCCAGCCAACTCAG

-258     TCGCATCCTCGGACAATTTGTTATCAAGGAACTCACCCAAAAACAAGCAAAGCTAGAAAA

-198     AGGTTGTGTGGCAGCCACCTAATGACATGAAGGACTGAAATTTCCAGCACACACAATGTA

-138     TCCGACGGCAATGCTTCTTCCACTGATCCGGAGAAGATAAGGAAACGAGGCAACCAGCGA

 -78     ACGTGAGCCATCCCAACCACATCTGTACCAAAGAAACGGGGCTATATATACCGTGGTGAC

 -18     CCGGCAATGGGGTCCTCAACTGTAGCCGGCATCCTCCTCTCCTCCGATAATACAAATACC
                          *↑**

 +43     ATG GCC CCC GCC GTG ATG GCT TCG TCG GCT ACC ACC GTC GCA CCC
          M   A   P   A   V   M   A   S   S   A   T   T   V   A   P
                                     -40

 +88     TTC CAG GGT CTC AAG TCC ACA GCC GGC CTG CCC GTC AGC CGC CGC
          F   Q   G   L   K   S   T   A   G   L   P   V   S   R   R
                -30                                     -20

+133     TCC ___ AGG GGC AGC CTC GGC AGC GTC AGC AAC GGC GGA AGG ATC
          S       R   G   S   L   G   S   V   S   N   G   G   R   I
                                     -10

+178     AGG TGC ATG CAG GTATGTTGGGGCACTAATTAAACTGATACGAGTTTCTTTGTCAG
          R   C   M   Q
                +1

+234     TGCAAGTAATTCACTTACAGAACATCCCCAATGTATATAACCAAACCCATCCTCGAAATA

+294     GGACCCATATACTGGAACTAAGTACAACCAAAGCTTTATTGATTGTGAACAACCCAGCAA

+354     TGCATATGAGAGCTGCCCATAAGGAGCAATTTTTGGCTTGTCGACTGATTTTTTCTAGCA

+414     TTGTTAGTACAATTAATTGACTCATCACCAAGTATTGAGCATCTGTTCGCATTCTATTCA

 +474    TTCAG GTG TGG CCA ATT GAG GGC ATC AAG AAG TTT GAG ACC CTG TCT
                V   W   P   I   E   G   I   K   K   F   E   T   L   S
                                           10

 +518     TAC TTG CCA CCC CTC TCC ACG GAA GCC CTC CTG AAG CAG GTC GAC
           Y   L   P   P   L   S   T   E   A   L   L   K   Q   V   D
                     20                                      30

 +563     TAC CTG ATC CGC TCC AAG TGG GTG CCC TGC CTC GAG TTC AGC AAG
           Y   L   I   R   S   K   W   V   P   C   L   E   F   S   K
                                           40
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Fig. 5B–11. Continued on next page.

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+608    GTT GGC TTC GTC TTC CGT GAG CAC AAC AGC TCT CCC GGG TAC TAC
         V   G   F   V   F   R   E   H   N   S   S   P   G   Y   Y
                    50                                      60

+653    GAC GGT CGA TAC TGG ACA ATG TGG AAG CTG CCT ATG TTC GGG TGC
         D   G   R   Y   W   T   M   W   K   L   P   M   F   G   C
                                        70

+698    ACC GAC GCC ACA CAG GTG CTC AAC GAG GTG GAG GAG GTC AAG AAG
         T   D   A   T   Q   V   L   N   E   V   E   E   V   K   K
                    80                                      90

+743    GAG TAC CCT GAC GCC TAT GTC CGC GTC ATC GGC TTC GAC AAC CTG
         E   Y   P   D   A   Y   V   R   V   I   G   F   D   N   L
                                        100

+788    CGC CAG GTG CAG TGC GTC AGC TTC ATC GCC TTC AGG CCA CCG GGT
         R   Q   V   Q   C   V   S   F   I   A   F   R   P   P   G
                    110                                     120

+833    TGC GAG GAG TCC GGC AAG GCC TAA ACTATGAGTTGAAACAATGGCCTATCTC
         C   E   E   S   G   K   A  OCHRE

+885    ATATGAAGATCTTTTGTGAACTTCACTTTTGTCCACGACCTCTGTTGCACGACTCTGCTT

+945    TCCGACCGGAGCATACCTTTTGTTCTATATGATTTGTGTATGTATGTAGGAACCTATGTC

+1005   TCGAGCATGCATACATAATTCCTCATAGGTCTATATACACCGGCTATCCATATGCAAAAC

+1065   CTGTGTAATATTTGTTATATACAACACGCGGACCATTGTCTTGCTGTTATTAATTCTTTT
                                                              *

+1125   TTCCCGCAAAAAAGGAAAAGTTTCTTTATTTGGCACTGCAATGGATATGCCTCACAGCTA

+1185   GTGGGTGGAGAATTCAGTATTTGACATTAAGATTCCCTGATTTGCAATTGCAAATTTCAG

+1245   TTTCTTTACTTATATCACTACAAAAGTCTTATTGTTTCTTTTCCACGTCATTACCATCTG

+1305   CTCCATTGGTTTTTGCTAGTAGAATAGGATGAAGCATGGACACAGATTAACTGAGCTCGA

+1365   GCTCATATGAGCTCGGGTGAACAATAAAATCTGAAAATACTTAGAAAGAATTCAAAATTT

+1425   TCTGTTTTTTGTGGCAAAATTTGACAAATGTTATAAATGCTTGCAAAGTTTCATCATAGA

+1485   ACGACATTCGTGGATGTCATGGCAAAAAACAAATTCAGCACTCTGAAAATAACTTTTTTG
          Cla I
+1545   AAGTATCG....3'  +1552
```

Fig. 5B–11. The nucleotide sequence of the gene for the small subunit of rubisco. The sequence of the gene and its surroundings was determined by Broglie et al. (1983) from the clone pWS4.3. The boxed sequences are possible control sequences (as discussed in the text) and the arrow marks the putative start of transcription. This is the position from which the numbers on the left-hand side start, −, before, and +, after. The protein-coding sequences are shown as triplets, with the amino-acid for which they code indicated by the standard one-letter abbreviation. The numbers underneath the sequence start at the N-terminal amino acid of the mature protein; however, the intervening sequence is not numbered as it is excised during the formation of the mature mRNA. The 3′-terminus of the mature mRNA is at nucleotide position +1120 (*). The polypeptide preceding the methionine at the +1 position is removed upon maturation of the translated protein.

Table 5B–2. Nucleotide sequences in the TATA box region of wheat genes.

Base pairs before start of transcription									Gene
−36	−35	−34	−33	−32	−31	−30	−29	−28	
T	A	T	A	T	A	T	A		
A	T	A	T	A	T	A	T		Rubisco
		T	A	T	T	T	A	A	
		A	T	A	A	A	T	T	Histone H3
		T	T	T	A	A			
		A	A	A	T	T			Histone H4
		T	A	T	A	A	A		
		A	T	A	T	T	T		Histone H4-variant
		(T A T A A A T A)							
		(A T A T T T A T)							Gliadin gene pW8233
		(T A T A A A T)							
		(A T A T T T A)							Gliadin gene α-1Y

III molecules to initiate transcription at the correct position. It also was noted that the 15 bp duplication near the middle of some of these genes (which, as noted above, appears to inactivate transcription) is in a region equivalent to that shown to be important in the control of transcription in *Xenopus borealis* (reviewed in Brown, 1984).

The second class of sequence is involved in the modulation of transcription. Messing et al. (1983) have reviewed the existence of various sequences common to plant genes that may play a role in the regulation of transcription but, at present, there is no experimental evidence defining such sequences in wheat. In the case of the ribosomal RNA genes, however, there is a short 132 to 134 bp sequence repeated at least 10 times preceding the point of transcription initiation (Fig. 5B–6). In *X. laevis*, this type of repetitive sequence has been shown by oocyte injection experiments to affect the efficiency of transcription initiation, particularly where rDNA units are competing for a limiting amount of RNA polymerase I (reviewed in Appels and Honeycutt, 1986). Although it is tempting to speculate that this also applies to wheat rDNA genes, there is no experimental evidence presently available to indicate that the 132 to 134 bp sequences belong to the second class of control sequence.

5B–5.3 The Translation Initiation Signal

All of the wheat genes so far analyzed utilize the codon ATG (methionine) to initiate translation of the messenger-RNA into a protein product. Many other plant genes also have a dinucleotide AA two bases upstream from the ATG codon and a G immediately downstream (Messing et al., 1983), and these could indicate a requirement for more than just the ATG codon for correct translation initiation (Kozak, 1981). However, the wheat genes so far analyzed do not feature the above nucleotides, either before or after the ATG codon (Fig. 5B–11).

5B–5.4 Internal Gene Structure

In addition to the introns discussed above, a feature of gene structure that is of interest in an evolutionary sense is the existence of internal repetition within the gene. For example, in the gliadin class I gene characterized by Rafalski et al. (1984), there are two identical 20 bp regions that appear to be part of a 147 bp region containing four related regions 36 bp in length. This is consistent with protein-sequencing studies (Kasarda et al., 1983) and suggests that sequence duplication has occurred within specific genes. The small RNA molecules from wheat, such as the 5.8S and tRNAs, show the conserved sequences and the modified bases found in other organisms (Dudock and Katz, 1969; Mackay et al., 1980; Ghosh et al., 1982; Barciszewska et al., 1983).

5B–5.5 Termination Signals

The wheat genes analyzed show that the universal nonsense codons TAA, TGA, and TAG are used to terminate translation of the polypeptide chain from the messenger RNA template. The messenger RNA transcript is itself terminated in an AT-rich region, which is beyond the nonsense codon, generating what has been called a 3′ untranslated region. The wheat genes coding for RUBISCO and class I gliadin protein generate messenger RNAs to which poly-A tails are added posttranscriptionally. In these genes, transcription termination is not well defined, but this generally occurs after the so-called poly-A addition signal; these are $\frac{AATATTT}{TTATAAA}$ and $\frac{AATAAA}{TTATTT}$, respectively. The messenger RNAs of histone genes do not generally show poly-A tails but do show sequences such as $\frac{ATTTA}{TAAAT}$, $\frac{AACAAA}{TTGTTT}$, and $\frac{AAAATA}{TTTTAT}$ after the translation termination codon that may contribute to specifying transcription termination. Certainly, termination of transcription of the wheat 5S genes occurs in an AT-rich region. In one of the clones isolated, the region has the sequence $\frac{TTTAAATTTTTTT}{AAATTTAAAAAAA}$ (Gerlach and Dyer, 1980). The actual point of transcription termination, or post-transcriptional cleavage, may be determined by the secondary structure adopted by the messenger RNA (Rafalski et al., 1984). In the gliadin gene, a region of RNA flanking the possible poly-A addition signal can adopt a hairpin structure and this may act as a termination signal by its interaction with the RNA polymerase II molecule.

5B–6 DNA IN CHLOROPLASTS AND MITOCHONDRIA

The DNA of chloroplasts and mitochondria is readily separated from nuclear DNA in that the organelles can be purified of nuclei before the DNA is isolated (Kolodner and Tewari, 1975; Vedel et al., 1976; Bowman and Dyer, 1982; Ogihara and Tsunewaki, 1982). The DNA of the chloroplast genome is circular and approximately 135 kb in length; the length estimates derive from both electron microscopic visualization of the mol-

ecule as well as restriction-endonuclease analyses. The DNA of mitochondria is also circular but length estimates are not consistent using the different techniques, apparently due to the presence of large repeats, inversions or deletions within the DNA of individual mitochondria (Leaver and Gray, 1982). Some heterogeneity may also derive from the existence of simple multiples of a basic unit of DNA (Palmer and Shields, 1984). Within the Triticeae, both chloroplast and mitochondrial DNAs appear to be conserved as judged from restriction-enzyme analyses.

5B–6.1 Chloroplast DNA (cpDNA)

Restriction-endonuclease digestion of the cpDNA from hexaploid wheat shows well-defined lengths of DNA (Vedel et al., 1976; Bowman et al., 1981, 1983; Ogihara and Tsunewaki, 1982; Tsunewaki and Ogihara, 1983). The various DNA fragments are designated depending on their length such that, for example, P1 is the longest PstI fragment and P13 the shortest. Fragments of identical lengths that co-migrate as a single band can be recognized by a quantitative increase in the UV fluorescence of the DNA stained with ethidium bromide (Vedel et al., 1980). These fragments also can be separated using two-dimensional electrophoretic procedures (Li and Liu, 1983). Lists have been prepared showing the fragment patterns after digestion with the various restriction enzymes (Bowman et al., 1981, 1983; Tsunewaki and Ogihara, 1983; Tsunewaki et al., 1985).

A complete map of cpDNA has been determined with respect to restriction-endonuclease sites and the positions of a number of chloroplast genes have been established (Fig. 5B–12). Genes that have been assigned to specific sites on the chloroplast genome include the 16S and 23S rRNA genes which are present on duplicate lengths of DNA, one inverted with respect to the other and separated by approximately 13 kb of single-copy DNA (Bowman et al., 1981). Other genes include *rbcL*, coding for the large subunit of RUBISCO (Bowman et al., 1981; Koller et al., 1982); the gene for cytochrome f (Willey et al., 1984) now designated *petA* (Hallick and Bottomley, 1983); the genes for the sub-units of ATP-synthetase, *atpA, atpB, atpE*, and *atpH*, respectively (Howe et al., 1982a, 1982b; 1983) and the gene for a thylakoid membrane protein, *psbA* (Bowman and Dyer, personal communication, 1984). The gene for chlorophyll *a* protein has also been located on the chloroplast genome (Smith and Gray, 1984) and the locations of 21 tRNA genes on various fragments of cpDNA have been reported (Mubumbila et al., 1985). The order of the nine tRNA genes occurring in the duplications is inverted consistent with the orientations of the 16S and 23S rRNA genes. The 13 kb single-copy region separating the duplications contains the $tRNA^{Leu}$ gene while 12 other tRNA genes have been located elsewhere in the cpDNA genome.

The DNA map of the chloroplast genome has been of particular interest in elucidating evolutionary relationships within the Triticeae since it is maternally inherited. There are few, if any, differences in the restric-

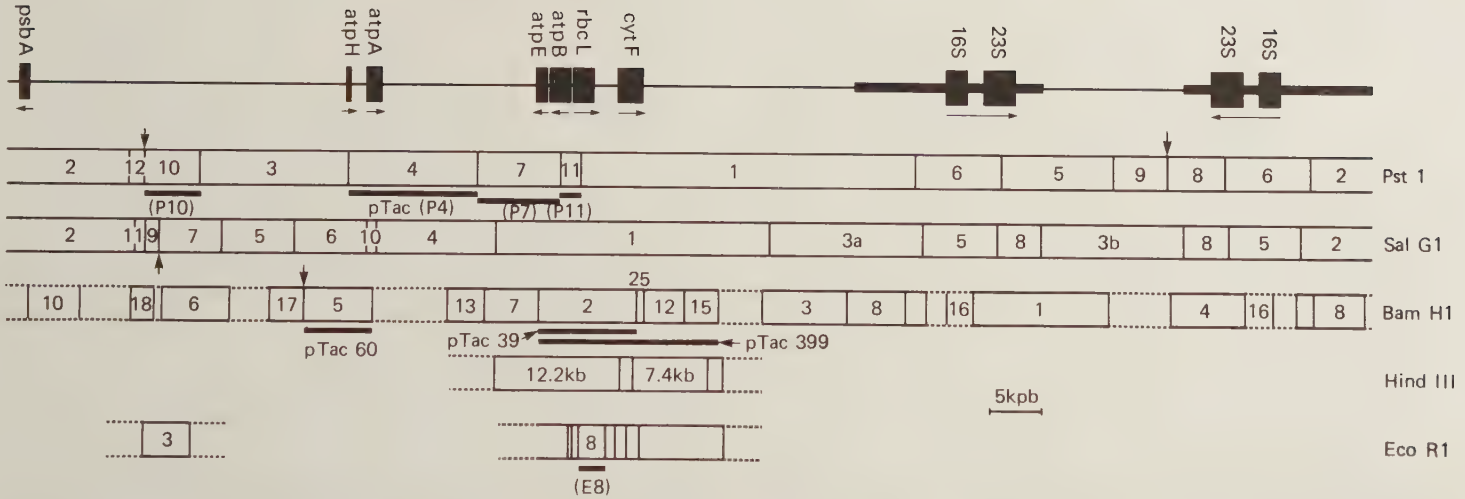

Fig. 5B–12. The chloroplast genome of wheat. The positions of structural genes and their directions of transcription are indicated and highlight the large inverted repeat involving the 16S and 23S rRNA genes. Restriction maps are shown for the restriction endonucleases PstI, SalGI, BamHI, HindIII, and EcoRI, and the heavy lines show cloned fragments with the names of the respective plasmids. The arrows mark restriction sites that have been lost in various members of the Triticeae. The map as presented is modified from Bowman et al. (1983) and C. M. Bowman and T. A. Dyer (Cambridge Plant Breeding Institute, personal communication, 1984). The latter have indicated that the entire chloroplast genome has now been cloned.

tion endonuclease map of cpDNA from different cultivars of *T. aestivum*. These include 'Capitole,' 'Moisson' (Vedel et al., 1980; 1981), 'Mardler,' 'Cappelle-Desprez,' 'Highbury' and 'Chinese Spring' (Bowman et al., 1983; Tsunewaki and Ogihara, 1983). In both euplasmic lines of diploid and tetraploid wheats and alloplasmic lines of wheat with diploid and tetraploid cytoplasms, the chloroplast genome of *T. aestivum* appears to be identical only to the cpDNA of *T. turgidum*, indicating that the tetraploid was the maternal parent of common wheat. While an alloplasmic line of wheat in *T. longissimum* cytoplasm appeared to have the same cpDNA as *T. turgidum* (Tsunewaki and Ogihara, 1983), this may well have been wrongly identified, because a euplasmic line of *T. longissimum* clearly differed (Bowman et al., 1983).

Among the *Triticum* spp., some 12 different cpDNA types have so far been recognized. In general, these have shown clear differences between and similarities within the A, B, G, and S genomes as defined by chromosomal and cytoplasmic studies (Tsunewaki, 1980). The hexaploid *T. aestivum* and the tetraploid *T. turgidum* have the identical B genome cpDNA type; *T. timopheevii*, *T. zhukovskyi*, and *T. araraticum* have the G type cpDNA genome in common; *T. searsii*, *T. speltoides*, *T. longissimum*, *T. bicorne*, and *T. kotschyi* have various modifications of the S type; *T. boeoticum*, *T. urartu*, and *T. monococcum* have variations of the A type; and *T. tauschii* has a unique D type (Bowman et al., 1983; Tsunewaki and Ogihara, 1983). The A and B types have not, so far, been found in the diploid relatives of wheat. Digests of the cpDNAs of barley, rye and oats also show similarities to those of wheat (Vedel et al., 1980).

As compared to the B genome cpDNA type of *T. aestivum*, the cpDNAs of other members of the Triticeae show differences in the lengths of many of the fragments, indicating the insertion or deletion of nucleotides. These insertions or deletions range between 50 and 1200 bp in size (Bowman et al., 1983; K. Tsunewaki, Y. Ogihara, and H. Tsujimoto, personal communication, 1984). Occasional losses of restriction-enzyme sites could well be due to point-mutation changes in the hexanucleotide recognition sequences (Fig. 5B–12). In the apparently more conserved regions of the genome, the hexanucleotide recognition sites are identical to those of wheat. Many of the differences have been found either in, or adjacent to, the segment of cpDNA present in the 5.2 kb P10 fragment and in the overlapping P7 and B2 fragments which, between them, contain approximately 15 kb of cpDNA (Fig. 5B–12).

5B–6.2 Mitochondrial DNA (mtDNA)

As indicated earlier, the multiplicity of bands and the occurrence of more than one fragment within bands after restriction-endonuclease digestion have so far precluded any attempts to map the mitochondrial genome. The surfeit of fragments implies that wheat (and higher plants generally) has a heterogeneous mixture of mtDNA molecules. The existence of large repeats, inversions or deletions (Leaver and Gray, 1982),

and simple multiples of a basic unit (Palmer and Shields, 1984) contribute to the heterogeneity. Methylation of restriction-endonuclease cleavage sites can block digestion of the DNA at a particular site and this could also contribute towards heterogeneity (Quetier and Vedel, 1980). On the other hand, when Bonen et al. (1980) digested mtDNA with the restriction-endonuclease isoschizomers MspI (insensitive to C-methylation), and HpaII (sensitive to C-methylation), they were unable to find evidence of methylation of the CCGG sequence. Nevertheless, methylation of DNA is a complex phenomenon (reviewed in Cooper, 1983) and cannot be ruled out as a potential contributor to the heterogeneity.

The mitochondrial genome of wheat encodes 18S and 26S ribosomal RNA genes as well as 5S RNA genes and a number of tRNAs (Cunningham et al., 1976; Bonen and Gray, 1980; Gray and Spencer, 1983). The 5S RNA genes are adjacent to the 18S rRNA genes (Falconet et al., 1984) but these are well separated from the 26S rRNA genes (Gray et al., 1982). In *S. cereale* mtDNA, a similar arrangement is found (Huh and Gray, 1982). The heterogeneity of wheat mtDNA is, once again, observed when radioactive 5S rRNA is used to probe restriction-endonuclease digests; a number of different DNA fragments show homology instead of the expected one or two well-defined fragments. Some fragments have been cloned into the plasmid pBR322. The SalI fragments S19 and S21 (6.2 and 5.5 kb, respectively) contain 5S and 18S rRNA genes with some tRNA genes. Except for the 700 bp difference in length, these two fragments appear to be identical (Leaver and Gray, 1982). Other structural information available for wheat mtDNA includes the sequences of the 5S RNA (Spencer et al., 1981) and $tRNA^{Phe}$ genes (Gray and Spencer, 1983), and the 18S rRNA gene (Spencer et al., 1984).

A number of comparative studies of the mtDNA from various members of the Triticeae have been made following the rationale already discussed for cpDNA. The mtDNA from different cultivars of *T. aestivum* are identical and *T. aestivum* mtDNA is identical to that of *T. turgidum*. The mtDNA of *T. timopheevii*, *T. speltoides*, *T. longissimum*, and *T. monococcum* are all distinctly different, as is the mtDNA of *T. ventricosum*. The latter, however, is very similar to that of *T. tauschii*. The mtDNAs of rye, barley, and oats show similarities with those of the wheats, and triticales have the mtDNA of their maternal parent (Vedel et al., 1978, 1980, 1981).

Lastly, it should be noted that there are many homologies between cp- and mtDNA (Lonsdale et al., 1983; Timmis and Scott, 1984) and often the homology between the chloroplast and mitochondrial genomes of a single species can be greater than the homology between cpDNAs of different species (Stern and Palmer, 1984). So far, these studies do not relate directly to the Triticeae but they do indicate an avenue for further exploration.

5B–7 GENETIC TRANSFORMATION IN WHEAT: PROSPECTS FOR THE FUTURE

The possibility of inserting novel DNA segments into wheat to provide new but specific characters as the need arises is an exciting area of research. In both plants and animals, this is now technically feasible (Frawley and Horsch, 1983; Herrera-Estrella et al., 1984). A particular problem in wheat, as in most monocotyledons, is that it has not been possible to regenerate plants from protoplast cultures. These are, at present, the required starting point for the introduction of new genetic material. Assuming that the technical difficulties of protoplast culture of wheat and the development of suitable DNA delivery systems (Flavell and Mathias, 1984) will be overcome, as is to be expected in light of the intensive worldwide efforts in this direction, we can consider the concurrent problem of isolating the genes of interest. It has been found that many genes have conserved sections of DNA sequences which allow them to be isolated using nucleic acid cross-hybridization. Thus, if a gene is isolated from one organism, related genes can be isolated from other organisms. As an example, several of the genes of wheat cpDNA were originally assayed using DNA sequences from other plants. This technique, therefore, enables individual genes to be recognized and isolated, and possibly modified and re-inserted. Novel, fully characterized genes such as storage proteins from nonrelated or dicotyledonous plants (or indeed, in the long run, genes from any organism whatsoever), may also be transferred to wheat and have the potential to be expressed. In the reciprocal sense, wheat genes themselves have been shown to cross wide barriers with the recent demonstration of a wheat α-amylase gene being introduced into yeast, in which the α-amylase was then expressed and secreted (Rothstein et al., 1984). Other characters, whether simple in the Mendelian genetic sense, such as disease resistance, or more complex, such as yield, presently lack defined gene products in molecular terms. The induction of new mRNA molecules in response to biological stress, such as fungal infections, has the potential to identify the range of genes involved in the reaction of a plant to fungal infection or similar stresses (for a recent example, see Cramer et al., 1985). Alternatively, the definition of the genes involved will come from a combination of genetics and molecular biology, examples of which follow. The *Rhizobium*/legume symbiotic relationship is biologically complex and to define the genes involved on the bacterial side of the relationship, transposon mutagenesis has been used (discussed in Scott et al., 1982). In short, the transposon Tn5 is a 5.6 kb DNA segment that inserts randomly into the DNA of the bacterium into which it is introduced and thereby causes mutations. In the search for *Rhizobium* genes involved in the symbiotic relationship, Tn5 is introduced by conjugation with an *E. coli* strain carrying the transposon, and successful transfers are assayed using the gene conferring

kanomycin resistance that is present on Tn5. The colonies of rhizobia carrying Tn5 are then screened for symbiotic mutants using a seedling assay. The mutants isolated are analyzed by producing a library of clones (see Fig. 5B–10), and the DNA in which the Tn5 is located is recovered by screening with a radioactive Tn5 probe. The DNA flanking the Tn5 segment defines the DNA of interest and provides a new probe for recovery of the gene involved in symbiosis from a *Rhizobium* that has not been exposed to Tn5. This approach to the isolation of a gene connected with a specific phenotype has also been employed in maize to recover the gene for bronze aleurone (*bz*). In this case, the transposable element was *Ac* (Fedoroff et al., 1984), a class of movable DNA first discovered in maize (reviewed in Fedoroff, 1984). It seems likely that, as soon as these types of transposable element are found or can be introduced into wheat, the genes that are correlated with particular phenotypes will be rapidly characterized.

5B–8 CONCLUSION

The studies of molecular biology and molecular genetics that have been summarized in this section indicate that a rapid and recent accumulation of knowledge about the molecular nature of the genomes of wheat and its relatives is taking place. Although the wheat genome is large, agronomically important segments of chromosomes are being selected for intensive study and, as assays for genes related to other phenotypes are discovered, these chromosomal segments will be gradually understood at the nucleotide sequence level. The genes and the chromosomes will then become suitable targets for genetic manipulation.

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5C Genetic and Biochemical Studies of Enzymes

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All plant species contain a large number of enzyme structural genes that are homologous to genes present in other plant species. Also, within many plant species, especially polyploids, two or more copies of many enzyme structural genes are present. Genetic and evolutionary findings from studies of these two classes of homologous genes in *Triticum aestivum* L. and other species of the Poaceae (Gramineae) tribe Triticeae are the subject of this section. Major emphasis will be placed on investigations that have provided information regarding chromosomal and genomic relationships. Studies of relationships among species also will be discussed briefly.

5C–1 PARALOGOUS AND ORTHOLOGOUS GENES

For any given enzyme, two or more molecular forms, called *isozymes*, often exist in a species. Most isozymes are genetically determined. They may result from the activity of different allelic forms of a gene (in which case they are called *allozymes*) or may be the products of homologous genes or of nonhomologous genes. Homologous genes present within a species are called *paralogous* (Fitch, 1970; Fitch and Margoliash, 1970). The possible modes of origin of paralogous genes are regional gene duplication events, aneuploidy, and polyploidy. Genes present in different species that descended from a common ancestral gene are also homologous; these are called *orthologous* (Fitch, 1970; Fitch and Margoliash, 1970). When a polyploid is formed following hybridization between two species, formerly orthologous genes become paralogous genes. Such paralogous genes will be referred to herein as members of *paralogous sets*, in order to distinguish them from paralogous genes that arose by mechanisms other than polyploidy. The term *homologous set*, or simply *set*, will also be used, to designate either a paralogous set or an orthologous group of genes.

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In order to discern evolutionary and phylogenetic relationships on the basis of the study of enzymes, homologous enzyme structural genes must be identified and the phylogenetic relationships among the genes determined. More specifically, to discern relationships among species (including relationships among chromosomes and genomes), orthologous structural gene loci must be identified, and to determine relationships among the chromosomes of the different genomes present in a polyploid species, paralogous sets of structural gene loci must be identified.

5C–2 CRITERIA FOR IDENTIFICATION OF HOMOLOGOUS GENES

When the products of only one structural gene are expressed for a given enzyme in a given tissue by different diploid Triticeae species, it may be concluded that the genes encoding the enzyme in the different species are orthologous. Also, when the products of no more than one structural gene are expressed by each genome in *T. aestivum* or other polyploid Triticeae species, it is quite likely that the genes are members of a paralogous set. (However, since inactivation of one or more members of any given paralogous set can occur [though the frequency with which this event has occurred in *T. aestivum* appears to be quite low—see below], the possibility must also be considered that the genes are the remaining active members of different paralogous sets rather than members of the same set.)

When two or more structural genes for a given enzyme are present in different diploid species and in other situations where the identity of homologous genes is not readily apparent, homologous genes can be identified by comparison of one or more properties of the enzymatic products of the genes or of the genes themselves. The chromosomal locations of the genes that encode a given enzyme (and the intrachromosomal locations of the genes, if known) may also aid in the identification of homologous genes. When two or more paralogous genes are identified in one or more of the genomes under study, the results of the aforementioned comparisons and the chromosomal or chromosome-arm locations of the genes will usually indicate the phylogenetic relationships among the genes.

5C–2.1 Properties of Protomers, Isozymes, and Genes

A number of properties of protomers, isozymes, and genes that can contribute evidence regarding homologous relationships among genes are listed in Table 5C–1. The properties are by no means equal in value in identifying homologous genes and determining phylogenetic relationships among them; in some cases it may be necessary to study several of them, as well as to have knowledge of the chromosomal or intrachromosomal locations of the genes being studied, in order to obtain sufficient evidence to assign genes to the same or to different paralogous and/or orthologous

sets. Two of the properties listed (the ability of protomers encoded by different genes to form oligomers, and the electrophoretic mobilities of isozymes) have played significant roles in identifying the members of a large number of Triticeae homologous gene sets. Studies of seven others (immunological properties, subcellular locations, tissue and developmental specificities, substrate specificities, quaternary structures, molecular weights, and isoelectric points of protomers or isozymes) have provided important evidence used in identifying the members of one to several gene sets.

Study of any one of the first six parameters listed in Table 5C–1 may provide sufficient evidence to allow a firm conclusion to be drawn regarding the homology or nonhomology of genes. The ability of protomers encoded by different genes to form oligomers is routinely assessed in aneuploid genetic studies of Triticeae isozymes, and relatively simple biochemical procedures can be used to determine the subcellular locations of isozymes. However, considerable expenditures of time and money are required to determine immunological properties, peptide compositions, and especially amino acid and nucleotide sequences. Therefore, it is unlikely that any of these four properties will be determined for more than a small number of Triticeae genes and isozymes in the near future.

Similarities among isozymes in electrophoretic mobility, tissue and developmental specificity, substrate specificity, response to inhibitors, or inducibility constitute evidence for homology among the genes that encode the isozymes. Differences in these properties are evidence against homology. Each of these properties must generally be considered along with other properties, because usually no one of them alone will provide definitive evidence for or against homology of genes.

It is unlikely that isozymes that differ in quaternary structure are encoded by homologous genes, and also unlikely that major differences in molecular weight exist among protomers encoded by homologous genes. The value of isozyme isoelectric points as indicators of Triticeae structural gene homology or nonhomology has not yet been adequately assessed. The small amount of information available suggests only that

Table 5C–1. Some properties of enzyme structural genes and of protomers and isozymes that can contribute evidence regarding the homology and/or nonhomology of Triticeae genes.†

Genes	
1. Nucleotide sequence.	8. Tissue and developmental specificity.
Protomers and Isozymes	9. Substrate specificity.
2. Amino acid sequence.	10. Response to inhibitors.
3. Ability of protomers encoded by different genes to form oligomers.‡	11. Inducibility.
4. Immunological properties.	12. Quaternary structure.
5. Peptide composition.	13. Molecular weight.
6. Subcellular location.	14. Isoelectric point.
7. Electrophoretic mobility.	

†Modified from MacIntyre (1976), Hart (1979b), and Tanksley (1983).
‡Applicable to oligomeric enzymes only.

when isozymic forms of an enzyme fall into two or more distinct groups with respect to their isoelectric points, members of different groups are probably not encoded by the members of one homologous gene set.

5C–2.2 Chromosomal and Intrachromosomal Locations of Genes

The chromosomes of the A, B, and D genomes of *T. aestivum* cv. Chinese Spring have been classified into seven homoeologous groups. The principal evidence for this classification is the demonstration that each chromosome in each genome can genetically compensate for a specific chromosome in each of the other two genomes (Sears, 1966b). The results of chromosome-pairing tests and the chromosomal locations of paralogous sets of genes support the classification. The chromosome arms of Chinese Spring have also been placed into homoeologous groups (Sears and Sears, 1979). In addition, various chromosomes and chromosome arms that belong to several other Triticeae genomes have been assigned to these groups, principally on the basis of the results of genetic-compensation tests (see Driscoll, 1983).

Since the criterion for placing Triticeae chromosomes and chromosome arms into homoeologous groups is genetic similarity, the finding that genes that encode isozymic forms of a given enzyme are located in different members of a homoeologous chromosome group (or, when telosomes are available, in different members of a chromosome-arm group) suggests that the genes are homologous. Likewise, the finding that isozymic forms of a given enzyme are encoded by genes that are located in different homoeologous groups suggests that the genes are not homologous, or at least that they belong to different gene sets. However, for some enzymes two or more sets of structural genes may be present in one homoeologous chromosomal or chromosome-arm group. Also, the tests used for placing chromosomes and chromosome arms into homoeologous groups, namely, tests of genetic compensation and chromosome pairing, are not sensitive enough to detect small translocation and inversion differences among the chromosomes and chromosome arms. Even among the members of the Chinese Spring homoeologous groups, which are known to consist of genetically highly similar chromosomes and chromosome arms, these differences may exist (Sears, 1966b; Hart, 1973; Gerlach et al., 1979). Consequently, orthologous genes in different species, and members of paralogous sets of genes in polyploids, may be present in chromosomes and chromosome arms that have been placed in different homoeologous groups. It is therefore apparent that, given the current state of knowledge of the genetic content of Triticeae chromosomes, the fact that genes located in different genomes are or are not located in chromosomes or chromosome arms that have been classified as homoeologous does not provide strong evidence regarding the homology or nonhomology of the genes.

Genetic-map positions have not yet played a role as indicators of homology (or of phylogenetic relationships) among any Triticeae enzyme structural gene loci. They have been reported for only nine loci in wheat, including two in genome A, three in genome B, and four in genome D (Hart et al., 1976; Nishikawa et al., 1981; Suseelan et al., 1982; Ainsworth et al., 1983; Chojecki et al., 1983; Gale et al., 1983), and in only one case for as many as two members of a homologous set (Nishikawa et al., 1981). It seems probable that in the future, in at least some cases, map positions will provide good evidence for gene homology. For example, the determination that presumptive homologous genes present in different genomes are located at similar map positions, close to several loci that are members of known homologous sets, would constitute good evidence that the genes are homologous. In a similar manner, evidence regarding the physical locations of enzyme loci within chromosome arms could aid in identifying homologous loci. However, to date, such evidence has been reported only for loci located in the p arms of wheat chromosomes 1B and 1D (Ainsworth, 1983; Ainsworth et al., 1984b).

In closing, it should be noted that genes designated as homologous cannot serve as evidence for homoeology among the chromosomes, chromosome arms, or segments in which they are located if a significant part of the evidence for their homology consists of their chromosomal or intrachromosomal locations.

5C–3 GENETIC AND BIOCHEMICAL CHARACTERIZATION OF TRITICEAE ENZYMES

The zymogram technique has been used to investigate the genetic control of a large number of Triticeae enzymes (Brown, 1983; Hart, 1983a; Hart and Tuleen, 1983b; Jaaska, 1983). Both electrophoresis (in starch and polyacrylamide gels) and isoelectric focusing (in polyacrylamide gels) have played prominent roles in these studies. Electrophoresis resolves isozymes into fractions on the basis of differences in their net charge and, to a lesser degree, their size and shape. As the name indicates, isoelectric focusing separates isozymes into fractions on the basis of differences in their isoelectric points. At least for some enzymes, e.g., glucosephosphate isomerase-1 (cf. Hart, 1979a; Chojecki and Gale, 1982) and β-amylase-1 and-2 (cf. Joudrier and Cauderon, 1976; Ainsworth et al., 1983), isoelectric focusing has considerably greater resolving power than electrophoresis. However, it is also a considerably more expensive technique than electrophoresis.

The chromosomal and chromosome-arm locations of Triticeae enzyme structural genes, both those of *T. aestivum* and of several diploid species, have been determined almost exclusively by studies of aneuploid strains derived in *T. aestivum* cv. Chinese Spring. Intergenomic variation

that is detectable with the zymogram technique is common among the members of paralogous isozyme structural gene sets in Chinese Spring; therefore, it has been possible to determine the chromosomal and chromosome-arm locations of genes simply by correlating variation in the level of expression of the products of genes with variation in the dosage of specific chromosomes and arms thereof. In most cases, the specific chromosomes in which genes are located were identified by study of the available compensating nullisomic-tetrasomic strains. The chromosome-arm locations were then determined by studying strains that contained ditelosomic derivatives of the identified chromosomes (Hart, 1979b, 1983a, 1984).

The chromosomal and chromosome-arm locations of enzyme structural genes in Triticeae relatives of *T. aestivum* have been determined by studies of wheat-alien disomic and ditelosomic chromosome-addition lines (Hart, 1979b; Brown, 1983; Hart and Tuleen, 1983b). For most enzymes studied, comparison of the zymogram phenotype of the parental wheat strain with that of the wheat–alien-species amphiploid has revealed the specific origin of each of the gene products expressed by the amphiploid and the addition lines, including protomers contained in hetero-oligomers. Confirmation of these findings and identification of the chromosome that contains the alien structural gene have been accomplished by identifying the chromosome-addition line that expresses the alien-gene product. For many alien genes located in chromosomes for which one or both of the possible ditelosomic chromosome-addition lines is available, the arm location of the gene has also been determined.

Wheat–alien-species translocation lines, telocentric chromosomes, Mendelian analyses, and intrachromosomal recombinant lines have been used to determine the genetic-map positions of eight enzyme structural gene loci in hexaploid wheat (Hart et al., 1976; Nishikawa et al., 1981; Ainsworth et al., 1983; Chojecki et al., 1983; Gale et al., 1983) and of one locus in tetraploid wheat (Suseelan et al., 1982). Linkage relationships among three closely linked esterase genes and two closely linked alcohol dehydrogenase genes have been determined in *Hordeum vulgare* L. by Mendelian analyses (Kahler and Allard, 1970; Brown, 1980).

For review of the literature on the biochemical characteristics of wheat isozymes, see Hart, 1983a. One or more molecular forms of several wheat enzymes have been purified, and comparative studies of one or more biochemical properties of different molecular forms have been reported for a few Triticeae enzymes. Of course, zymogram studies themselves provide evidence regarding some properties of isozymes, e.g., their quaternary structure (see pages 42 and 43 in Hart, 1983a) and, for enzymes studied with isoelectric focusing, their isoelectric points. Characterization of purified isozymes encoded by homologous Triticeae genes with known chromosomal locations in different genomes and species has been reported for only one enzyme, alcohol dehydrogenase-1 (Langston et al., 1979, 1980).

5C–4 RELATIONSHIPS AMONG TRITICEAE CHROMOSOMES

5C–4.1 Chromosomes of Genomes A, B, and D of *Triticum aestivum* cv. Chinese Spring

Table 5C–2 lists enzyme structural gene loci whose chromosomal locations have been determined in Chinese Spring. Also shown are the enzymes that the genes encode and their Enzyme Commission numbers. Twenty-seven of the enzymes listed in Table 5C–2 are encoded by paralogous sets composed of three gene loci. Paralogous sets composed of two loci have been identified for five enzymes, namely, β-AMY-1, EST-3, HK-1, PER-1, and PGM-1. An active *β-Amy-B1* gene was not detected in a study of 45 hexaploid wheat cultivars (Ainsworth et al., 1983) and an active *Est-A3* gene was not detected in a study of 208 accessions (Jaaska, 1980). This suggests that active forms of these genes are not present, or are present at only a low frequency, in hexaploid wheat. However, it is also possible that active genes are present and that their products co-focus or co-electrophorese with the products of genes located in different chromosomes. A third active structural gene locus may well be present in Chinese Spring for both HK-1 and PER-1, since the genetic basis of most of the isozymes expressed in the tissues from which these enzymes were extracted for study (mature dry grains for HK and flag leaves for PER) has not been determined. It is probable that Chinese Spring PGM-1 is encoded by a paralogous set composed of three active loci, but the A-genome member of the set has only been tentatively identified. *β-Amy-A2* and *Hk-B2* are loci assigned homologous set designations for which no paralogous loci have been detected in Chinese Spring. For the same reason as stated above for HK-1 and PER-1, one or more additional active HK-2 structural gene loci may well be present in Chinese Spring. The presence of one or more additional active β-AMY-2 loci seems less likely since only *β-Amy-A2* was detected in a study of 45 hexaploid wheat cultivars (Ainsworth et al., 1983).

Analyses of intrachromosomal recombinant lines and of F_2 progenies obtained from crosses between cultivars carrying different alleles have provided evidence that the loci designated *α-Amy-B2*, *β-Amy-A2*, *β-Amy-D1*, *Est-A5*, *-B5*, and *-D5*, and *Gpi-D1* each produce several isozymes (Ainsworth et al., 1983; 1984a; Chojecki et al., 1983; Gale et al., 1983). These loci may be complex, i.e., they may contain two or more tightly linked structural genes. Alternatively, post-translational modification of the product of a single gene may be the cause of the production of more than one molecular form by one or more of these loci. Findings consistent with genetic recombination within a complex locus containing more than one structural gene have been reported for *α-Amy-B2* (Gale et al., 1983) and *Est-B5* (Ainsworth et al., 1984a).

The chromosome-arm locations of the paralogous sets of gene loci

Table 5C–2. Enzyme structural gene loci whose chromosomal locations have been determined in *Triticum aestivum* cv. Chinese Spring.

Gene loci†	Enzyme encoded	Enzyme Commission number of enzyme	References‡
Acph-1 set	Acid phosphatase-1	3.1.3.2	15,19
Aco-1 set	Aconitase-1	4.2.1.3	11
Aco-2 set	Aconitase-2	4.2.1.3	11
Adh-1 set	Alcohol dehydrogenase-1	1.1.1.1	14,15,19
Amp-1 set	Aminopeptidase-1	3.4.11.-	15,19
α-Amy-1 set	α-Amylase-1	3.2.1.1	13,30,31
α-Amy-2 set	α-Amylase-2	3.2.1.1	13,30,31
α-Amy1	α-Amylase	3.2.1.1	31
β-Amy-1 set	β-Amylase-1	3.2.1.2	2,23
β-Amy-A2	β-Amylase-2	3.2.1.2	2
Aadh-1 set	Aromatic alcohol dehydrogenase-1	1.1.1.91	21
Aadh-2 set	Aromatic alcohol dehydrogenase-2	1.1.1.90	18
Ep-1 set	Endopeptidase-1	3.4.21-24.-	19
Est-1 set	Esterase-1	3.1.1.-	5,6,10
Est-2 set	Esterase-2	3.1.1.-	22
Est-3 set	Esterase-3	3.1.1.-	22
Est-4 set	Esterase-4	3.1.1.-	22,27
Est-5 set	Esterase-5	3.1.1.-	3,26
Gpi-1 set	Glucosephosphate isomerase-1	5.3.1.9	12,17
Got-1 set	Glutamic oxaloacetic transaminase-1	2.6.1.1	16
Got-2 set	Glutamic oxaloacetic transaminase-2	2.6.1.1	16
Got-3 set	Glutamic oxaloacetic transaminase-3	2.6.1.1	16
Hk-1 set	Hexokinase-1	2.7.1.1	1
Hk-B2	Hexokinase-2	2.7.1.1	1
Lpx-1 set	Lipoxygenase-1	1.13.11.12	19
Lpx-2 set	Lipoxygenase-2	1.13.11.12	19
Mdh-1 set	Malate dehydrogenase-1	1.1.1.37	9
Ndh-1 set	NADH dehydrogenase-1	1.6.99.3	20
Per-1 set	Peroxidase-1	1.11.1.7	4,27
Per1, 2, & 3	Peroxidase	1.11.1.7	8,24,25
Pde-1 set	Phosphodiesterase-1	3.1.4.1	33,34
Pgm-1 set	Phosphoglucomutase-1	2.7.5.1	7
Skdh-1 set	Shikimate dehydrogenase-1	1.1.1.25	26,28
Sod-1 set	Superoxide dismutase-1	1.15.1.1	29
Tpi-1 set	Triosephosphate isomerase-1	5.3.1.1	32
Tpi-2 set	Triosephosphate isomerase-2	5.3.1.1	32

†Gene loci are designated with symbols consistent with "Recommended Rules for Gene Symbolization in Wheat" (McIntosh, 1983). Synonyms which appear in the literature for some of the loci are given in Hart (1983a, 1984). The *Acph-1* loci were formerly designated *Acph2* to *6* and *8* (Hart and Langston, 1977), the *Aadh-1* and *-2* loci as *Adh-2* and *-3*, respectively, and *α-Amy1* as *α-Amy2* (see Hart, 1983a, 1984).

‡References: (1) Ainsworth, 1983; (2) Ainsworth et al., 1983; (3) Ainsworth et al., 1984a; (4) Ainsworth et al., 1984b; (5) Barber et al., 1968; (6) Barber et al., 1969; (7) Benito et al., 1984; (8) Benito and Perez de la Vega, 1979; (9) Benito and Salinas, 1983; (10) Bergman, 1972; (11) Chenicek, 1984; (12) Chojecki and Gale, 1982; (13) Gale et al., 1983; (14) Hart, 1970; (15) Hart, 1973; (16) Hart, 1975; (17) Hart, 1979a; (18) Hart, 1983b; (19) Hart and Langston, 1977; (20) Hart and Tuleen (unpublished); (21) Jaaska, 1978b; (22) Jaaska, 1980; (23) Joudrier and Cauderon, 1976; (24) Kobrehel, 1978; (25) Kobrehel and Fiellet, 1975; (26) Koebner and Shepherd, 1983; (27) May et al., 1973; (28) Neuman and Hart, 1983; (29) Neuman and Hart, 1986; (30) Nishikawa and Nobuhara, 1971; (31) Nishikawa et al., 1981; (32) Pietro and Hart, 1985; (33) Wolf and Rimpau, 1979; (34) Wolf et al., 1977.

listed in Table 5C–2 are shown in Table 5C–3. This table shows that the members of each of the 32 sets of paralogous gene loci that have been identified in Chinese Spring are located in homoeologous chromosomes. Also, with one possible exception (the *Sod-1* set; see below), the members of each set are located in chromosome arms that are considered to be homoeologous. The evidence that *Hk-B1* and *Hk-D1* are members of a paralogous set consists only of the location of the loci in homoeologous chromosome arms. For the gene loci that comprise each of the other 31 sets, however, from one to several other kinds of evidence—in most cases quite strong, in a small number of cases fairly weak—support the designation of the loci as members of paralogous sets. Consequently, the chromosome-arm locations of these gene loci provide good support for the proposal, first suggested by the results of tests of genetic compensation (Sears, 1954, 1966b), that the gene synteny relationships that existed in the ancestral *Triticum* genome are, in large part, conserved in the three genomes of Chinese Spring. Furthermore, conservation of the genetic content of chromosome arms is also indicated. The evidence is strongest for homoeologous groups 3, 4, and 6, in which from two to five paralogous sets of gene loci are located in each arm group, for the 5q group, in which four paralogous sets composed of three loci are located, and for group 1, where conservation is indicated both by the gene locations shown in Table 5C–3 and by the presence of a member of a paralogous set of gliadin structural gene loci at the same map position in each 1p arm and of a member of a paralogous set of glutenin structural gene loci at the same map position in each 1q arm (Rybalka and Sozinov, 1979; Lawrence and Shepherd, 1981b; Payne et al., 1982; Chojecki et al., 1983).

Table 5C–3. Chromosome-arm locations of paralogous sets of enzyme structural gene loci in genomes A, B, and D of *Triticum aestivum* cv. Chinese Spring.†

Chromosome-arm group‡	Paralogous sets	Chromosome-arm group‡	Paralogous sets
1p	*Gpi-1, Hk-1*§¶, *Per-1*¶	1q	*Mdh-1*
2S	None	2L	*Sod-1*
3p	*Est-1, Pde-1, Tpi-1*	3q	*Est-2*#, *Est-5, Got-3*
4p	*Adh-1, Lpx-1, Ndh-1, Pgm-1*¶	4q	*Acph-1, β-Amy-1*††
5p	*Skdh-1*	5q	*Aadh-1, Aco-2, Lpx-2, Tpi-2*
6p	*Amp-1, Got-1*	6q	*Aadh-2, Aco-1, α-Amy-1, Est-4, Got-2*
7p	*Est-3*¶	7q	*α-Amy-2, Ep-1*

†See Table 5C–2 for references. The other identified Chinese Spring enzyme structural gene loci and their chromosome-arm locations are *Hk-B2* in 3Bp, *Per2* in 4Bp, *β-Amy-A2* in 5Aq, *α-Amy1* in 6Bq, *Per3* in 7Ap, and *Per1* in 7Dp.

‡Chromosome arms are designated p and q, consistent with the recommendations in Sears and Sears (1979), except for group 2, in which S and L designate the short and long arms of the chromosomes, respectively.

§The evidence that the two loci comprising this set are the members of a paralogous set is the location of the loci in homoeologous chromosome arms.

¶An A-genome locus has not been identified for this set.

#The chromosome-arm location of *Est-A2* has not been reported.

††A B-genome locus has not been identified for this set.

For most Chinese Spring homoeologous groups, tests have been conducted of the ability of telosomes derived from homoeologous chromosomes to pair either with each other or with an intact homoeologue when the effect of the *Ph1* locus is suppressed (Riley and Chapman, 1964; Sears and Sears, 1979; Riley and Chapman, personal communication cited in Sears and Sears, 1979, p. 403). Formation of a trivalent by two such telosomes and a homoeologue indicates that the two telosomes are not homoeologous. Only one anomaly exists between the results of these tests and the gene locations shown in Table 5C–3. In the only test conducted that has provided critical evidence regarding the relationships of the arms of 2B to those of 2A and 2D, evidence was obtained that 2BL and 2DL are not homoeologous. The evidence consists of formation of a trivalent composed of 2BL, 2DL, and a homoeologue in several meiocytes (Sears and Sears, 1979; L.M.S. Sears, personal communication, University of Missouri, Columbia, 1979). Homoeology of 2BS and 2DL and of 2BL with 2DS is inconsistent with the presence of a paralogous set of *Sod-1* gene loci in the long arms of the group 2 chromosomes. The evidence that the SOD gene loci comprise a paralogous set is not conclusive. However, a small pericentric inversion in 2B could also be the cause of the anomaly. Inversion of a segment containing *Sod-B1* following a break close to the centromere in 2BS and a break somewhat further from the centromere and distal to *Sod-B1* in 2BL would produce a new long arm consisting of some former 2BL genetic material (including *Sod-B1*) near the centromere, but mostly of genetic material from the old 2B short arm. Presumably, this arm as a telosome would readily pair with the short arm of a homoeologue when the effect of *Ph1* is suppressed. A pericentric inversion in 4B may be the cause of the homoeology of 4BS and 4BL with 4DL and 4DS, respectively (Gerlach et al., 1979; see also Hart, 1973).

5C–4.2 Chromosomes of Genomes E, H, R, and S[1]

In four diploid Triticeae species, namely, *Elytrigia elongata* (Host) Holub, *Hordeum vulgare* L., *Secale cereale* L., and *T. longissimum* (Schweinf. & Musch.) Bowden, chromosomal locations have been determined for from 15 to 20 enzyme structural gene loci that are orthologous to gene loci with known chromosomal locations in Chinese Spring. The locations of these gene loci, along with those of the orthologous Chinese Spring loci, are shown in Table 5C–4. The loci are not distributed evenly among the chromosomes in the four species. In each of the species, from four to five loci have been located in chromosome 6, from three to five loci in chromosome 3, and from two to five loci in chromosome 5. In contrast, only one locus has been identified in chromosome 2 among all of the species and, in chromosomes 1, 4, and 7 combined, only one locus has been identified in *T. longissimum* and only from six to eight loci in each of the other three species. Nevertheless, the locations of the loci reveal a good deal about the synteny relationships of genes in Triticeae genomes.

Synteny relationships among the members of the orthologous groups of gene loci of genomes A, B, D, E, H, and S^1 that are listed in Table 5C–4 are, with only one exception, conserved. *Aco-E2* is located in 4EL, while the *Aco-2* locus in each of the genomes A, B, D, R, and S^1 is located in chromosome 5. Chromosome-arm locations have been determined for 14 *E. elongata* loci, 2 *H. vulgare* loci, and 1 *T. longissimum* locus. These also are conserved, again with the exception of *Aco-E2*.

The *Aco-2* locus is syntenic with the *Aadh-1* and *Lpx-2* loci in genomes A, B, and D, but is located in a different chromosome from these loci in the wheat–*E. elongata* chromosome-addition line series. This suggests that *Aco-2* was located distal to *Aadh-1* and *Lpx-2* in the q arm of chromosome 5 in the genome ancestral to genomes A, B, D, and E and is currently in this position in chromosome 5 in genomes A, B, and D. It is quite unlikely that the indicated translocation difference, which involves noncentromeric chromosome breaks, arose during the development of the wheat–*E. elongata* chromosome-addition lines, but whether it occurs naturally throughout *E. elongata* is unknown.

Chromosomal locations have been determined for approximately 15 *H. vulgare* enzyme structural gene loci in addition to those shown in Table 5C–4 (summary in Brown, 1983). Several of these loci are clearly not orthologous to any Chinese Spring locus whose chromosomal location has been determined. However, a number of others probably are, among them being several *Est* loci and one *β-Amy* and one *Ndh* locus. With the exception of *Est-5*, there is insufficient information available to suggest probable orthologous relationships between specific barley and wheat *Est* gene loci. However, sufficient evidence is available to make it probable that the *β-Amy* and *Ndh* gene loci present in chromosome 4 of cultivar Betzes are orthologous to the *β-Amy-1* and *Ndh-1* loci located in the 4q and 4p arms, respectively, of Chinese Spring.

Koller and Zeller (1976) have proposed that *S. cereale* differs from its presumptive ancestor *S. montanum* Guss and from Chinese Spring by interchanges between the presumptive ancestral chromosome arms 7RS and 4RL and between the arms 7RL and 6RL. The enzyme gene locations that have been determined in Chinese Spring and *S. cereale* support this proposal but also provide evidence for another interchange. The Chinese Spring *Adh-1* gene loci are located in the 4p arms and the *S. cereale Adh-1* locus is in the short arm of chromosome 4R. *Acph-1* gene loci are located in the Chinese Spring 4q arms and the *S. cereale Acph-1* locus is located in the short arm of chromosome 7R. This is consistent with a 4RL-7RS interchange. The *Ep-1* gene loci of Chinese Spring are in the 7q arms and the *Aadh-2* and *Got-2* loci in the 6q arms. *Ep-R1*, *Aadh-R2*, and *Got-R2* are in 6R. This is consistent with a 7RL-6RL interchange following a chromosome break distal to *Aadh-R2* and *Got-R2* in the ancestral 6RL and a break proximal to *Ep-R1* in the ancestral 7RL. The *Est-5* loci of Chinese Spring are in the 3q arms, the *Est-5* locus of *S. cereale* is in 6R, and the *Est-5* locus of *S. montanum* is in

Table 5C–4. Chromosomal locations of orthologous enzyme structural gene loci in the genomes of *Triticum aestivum* cv. Chinese Spring, *Elytrigia elongata*, *Hordeum vulgare* cv. Betzes, *Secale cereale* cv. Dakold and/or Imperial and/or King II, and *Triticum longissimum*.†

Gene loci	Genomes				
	A, B, & D (*T. aestivum*)	E (*E. elongata*)	H (*H. vulgare*)	R (*S. cereale*)	S^l (*T. longissimum*)
Gpi-1	1p	1S	1S	1(I,K)‡	1
Per-1	1p	--	--	1(K)	--
Mdh-1	1q	--	1L	1L(D,I,K)	--
Sod-1	2L	--	--	2(I)	--
Est-1	3p	3S	--	3(I)	3
Hk-2	3p	3S§	--	--	--
Pde-1	3p	--	--	--	3S
Tpi-1	3p	3	3	3(D,I)	3
Est-5	3q	--	3	6L(D,I,K)	3
Got-3	3q	3L	3	3(I)	3
Adh-1	4p	4S	4	4S(I,K)	--
Lpx-1	4p	4S	4	--	--
Pgm-1	4p	--	4	4S(D,I,K)	--
Acph-1	4q	--	4	7S(I)	--
Skdh-1	5p	--	5	5S(I)	5
Aadh-1	5q	5L	--	5(I)	5
Aco-2	5q	4L	--	5(K)	5
Lpx-2	5q	5L	--	--	5
Tpi-2	5q	--	5	5(D,I)	5
Amp-1	6p	6α	6	6(I)	6
Aadh-2	6q	6β	6	6(I)	6
Aco-1	6q	6β	6	--	6
α-Amy-1	6q	6	6	--	--
Got-2	6q	6β	6	6(I)	6
α-Amy-2	7q	7	7	7L(I,K)	--
Ep-1	7q	7L	7	6(I)	--
Ref.	a	b	c	d	e

†Related chromosomes in genomes A, B, D, E, H, R, and S^l are assigned the same number, with Chinese Spring accepted as having the standard chromosome arrangement (McIntosh, 1983). Since three or more translocation differences exist between *S. cereale* and Chinese Spring, the designations assigned to some R genome chromosomes, especially 4 and 7—which differ from their Chinese Spring homoeologues by a large reciprocal translocation—are by and large arbitrary (Koller and Zeller, 1976; Sybenga, 1983). The arms of the chromosomes in genomes A, B, and D, with the exception of homoeologous group 2, are designated p and q to indicate homoeologies (Sears and Sears, 1979) and those in homoeologous group 2 and in the other genomes S (= short) and L (= long) or, if relative arm lengths are not known, α and β, α designating the arm first isolated as a telosome (McIntosh, 1983).

‡D = Dakold, I = Imperial, and K = King II.

§The evidence for orthology of *Hk-B2* and *Hk-E2* is the location of the loci in homoeologous chromosome arms.

(continued on next page)

$6R^m$ (Ainsworth et al., 1986). These gene locations indicate that the latter two species differ from Chinese Spring by a translocation involving chromosomes 3 and 6. The synteny relationships among the seven gene loci

Table 5C–4. Continued

References

a. See Table 6.

b. *Aco-1* and *-2*, Chenicek, 1984; *α-Amy-1* and *-2*, Ainsworth and Gale, 1986; *Hk-2*, Ainsworth, 1983; *Tpi-1*, Pietro and Hart, 1985; others, Hart and Tuleen, 1983a.

c. *Acph-1*, *Gpi-1*, *Mdh-1*, Powling et al., 1981; *Aco-1*, Brown and Munday, 1982, Chenicek, 1984; *Adh-1*, *Amp-1*, *Got-2*, *Ep-1*, Hart et al., 1980; *Aadh-2*, *Lpx-1*, *Skdh-1*, Hart and Tuleen, unpublished; *α-Amy-1* and *-2*, Brown and Jacobsen, 1982; Muthukhrishnan et al., 1984; *Est-5*, Ainsworth et al., 1986; *Got-3*, Brown and Munday, 1982; Hart and Tuleen, unpublished; *Pgm-1*, Benito et al., 1985; *Tpi-1* and *-2*, Pietro and Hart, 1985.

d. *Acph-1*, Tang and Hart, 1975; Hart 1978; *Aco-2*, Chenicek, 1984; *Adh-1*, Irani and Bhatia, 1972; Tang and Hart, 1975; Hart, 1978; *Aadh-1* and *-2*, *Amp-1*, *Ep-1*, Hart and Tuleen, unpublished; *α-Amy-1* and *-2*, Ainsworth and Gale, 1986; *Est-1*, Barber et al., 1968, 1969; *Est-5*, Ainsworth et al., 1986; *Got-2* and *-3*, Tang and Hart, 1975; *Gpi-1*, Chojecki and Gale, 1982; Hart and Tuleen, unpublished; *Mdh-1*, Salinas and Benito, 1985a; *Per-1*, Ainsworth et al., 1984b; *Pgm-1*, Salinas and Benito, 1985b, Wehling et al., 1985; *Skdh-1*, Koebner and Shepherd, 1983; *Sod-1*, Neuman and Hart, 1986; *Tpi-1* and *-2*, Pietro and Hart, 1985.

e. *Aco-1* and *-2*, Chenicek, 1984; *Est-5*, Ainsworth et al., 1986; *Pde-1*, Ceoloni and Galili, 1982; *Tpi-1* and *-2*, Pietro and Hart, 1985; others, Hart and Tuleen, 1983c, unpublished.

located in chromosomes 1R and 5R are identical to those of orthologous Chinese Spring loci.

Most *E. elongata* and *H. vulgare* chromosomes have been substituted for one or more members of a *T. aestivum* homoeologous chromosome group (see Driscoll, 1983). The vigor and fertility of the plants obtained have been sufficiently similar to the vigor and fertility of euploid wheat plants to indicate that the substituted alien chromosome is genetically highly similar to the missing wheat chromosome. Similar evidence for homoeology with the members of a wheat homoeologous chromosome group has been obtained for *S. cereale* chromosomes 1R, 2R, 3R, 5R, and 6R (see Driscoll, 1983) and for chromosomes $1S^{l}$, $2S^{l}$, $3S^{l}$, $5S^{l}$, and $6S^{l}$ of *T. longissimum* (Tuleen and Hart, unpublished).

The results of the aforementioned genetic-compensation tests and the chromosomal locations of orthologous genes complement one another in defining the homoeologous relationships of the chromosomes of genomes E, H, R, and S^{l} to those of Chinese Spring and to each other. The compensation tests have provided strong evidence that most E, H, R, and S^{l} genome chromosomes are, in large part, conserved in their genetic content relative to each other and to the genomes of Chinese Spring. The enzyme structural gene locations have provided evidence at the genic level for this conservation. They have also provided evidence regarding translocation differences between genomes E (Chenicek, 1984) and R (Tang and Hart, 1975; Koller and Zeller, 1976; Hart, 1978; Ainsworth et al., 1986) relative to one another and to the other genomes.

5C–4.3 Chromosomes of Genomes H^{ch}, R^{m}, and U

The data available for *H. chilense* Roem. & Schult. (genome H^{ch}), *S. montanum* (R^{m}), and *T. umbellulatum* (Zhuk.) Bowden (U) are insuffi-

cient to allow most of the chromosomes in these species to be firmly identified relative to the standard set of Triticeae chromosomes present in *T. aestivum* cv. Chinese Spring. However, the few data that are available are by and large in agreement and support the hypothesis that the ancestral Triticeae gene synteny relationships are largely conserved in these genomes. A *Gpi-1* locus (Chojecki and Gale, 1982) and a *Per-1* locus (Ainsworth et al., 1984b) have been located in chromosome G of *H. chilense* (a high-molecular-weight glutenin locus has also been identified in chromosome G; see Miller et al., 1982b). A *Gpi-1* locus has also been located in both *S. montanum* chromosome $1R^m$ and *T. umbellulatum* chromosome 1U (Chojecki and Gale, 1982). An *Est-5* locus has been located in chromosome $3H^{ch}$ of *H. chilense* and, as noted above, in chromosome $6R^m$ of *S. montanum* (Ainsworth et al., 1986). A *Skdh-1* locus (Koebner and Shepherd, 1983) and a *Tpi-2* locus (Pietro and Hart, 1985) have been identified in chromosome 5U of *T. umbellulatum*. $6R^mL$ of *S. montanum* has been shown to contain an *α-Amy-1* locus, and an *α-Amy-2* locus has been located in $7H^{ch}\beta$ of *H. chilense*, $7R^mL$ of *S. montanum*, and 7U of *T. umbellulatum* (Ainsworth and Gale, 1986). With the exception of the *Est-*R^m*5* locus of *S. montanum*, the synteny relationships among the aforementioned loci are identical to those of orthologous loci in Chinese Spring. Chromosome-substitution evidence for wheat-alien chromosome homoeology has been obtained for *H. chilense* chromosome $7H^{ch}$, for *S. montanum* chromosomes $1R^m$, $2R^m$, and $6R^m$, and for *T. umbellulatum* chromosomes 1U, 2U, 5U, and 7U (see Driscoll, 1983).

5C–5 RELATIONSHIPS AMONG SPECIES

The origins of the genomes present in the cultivated wheats and a number of other phylogenetic relationships among Triticeae spp. have been investigated by studying enzymes with the zymogram technique. Most investigations have been conducted on enzymes for which there is good evidence for the presence of one structural gene locus per genome in Triticeae spp. In the study of a given enzyme, the evidence obtained regarding the donor of a genome to a polyploid species is strongest when a survey of a large number of accessions collected from throughout the range of the species discloses that one allele is fixed in the genome of interest in the polyploid species and that the same allele is present in only one of the likely progenitors. But even this finding must be viewed with caution, since alleles can be lost from species due to selection and chance, and can be introduced into species by introgression and mutation.

In seeking to identify the donors of genomes to *T. turgidum* L. *sensu lato* and *T. aestivum*, Jaaska (1976, 1978b, 1980, 1981) has studied several enzymes whose genetic bases in the Triticeae are well established. These include AADH-1, ADH-1, EST-1, -2, -3, and -4, and GOT-1, -2, and -3. Only a few of the enzymes contributed evidence regarding the donor of

any one genome, but the evidence obtained consistently supports an ancestor of *T. speltoides* (Tausch) Gren. ex Richter as the B-genome donor and ssp. *strangulata* of *T. tauschii* (Coss.) Schmalh. as the D-genome donor. Only one *Got-B2* allele and only one *Got-B3* allele were found in *T. turgidum* and *T. aestivum*; only *T. speltoides* among species of the Sitopsis section was found to possess both alleles. Also, the *Aadh-B1* allele detected in the polyploid wheats was found only in *T. speltoides* among all of the diploid *Triticum* spp. examined, and the *Est-B2* allele of the polyploid wheats was found only in *T. speltoides* among species of the Sitopsis section. The only *Adh-D1* and *Got-D2* alleles found in the polyploid wheats were found only in *T. tauschii* ssp. *strangulata*. In a study of variation in an acid phosphatase in sympatric populations of four allotetraploid *Aegilops* spp. that share certain genomes, Jaaska (1978a) found no evidence for widespread introgression among the species.

Nakai (1979a, 1979b, 1981, 1982) has investigated the origin of the B genome and several other phylogenetic relationships by studying the EST-5 enzymes. Observing that one EST-5 zymogram phenotype was expressed by 67% of the tetraploid wheat strains studied and that the B-genome component of this phenotype was similar to that expressed by several species of the Sitopsis section, he concluded that an ancestor of a member of the Sitopsis section probably contributed the B genome to polyploid wheats. Nakai also determined the probable EST-5 zymogram phenotypes of the donors of the D genome to *T. crassum* (Boiss.) Aitch. & Hensl., *T. syriacum* Bowden, *T. cylindricum* Ces., and hexaploid wheat.

Nishikawa et al. (1980) have studied α-AMY isozyme variation in seeking evidence regarding the origin of hexaploid wheat. They found that accessions of *T. tauschii* collected near Gorgan, in Iran, southeast of the Caspian Sea, express the three α-AMY isozymes most frequently observed to be produced by the D genome in hexaploid wheat. On this basis, they concluded that this region should be added to those previously considered as possible birthplaces of hexaploid wheat.

5C–6 CONCLUDING REMARKS

Evidence regarding the identification of alien chromosomes, chromosome arms, and chromosome segments relative to the standard set of Triticeae chromosomes present in *T. aestivum* cv. Chinese Spring can be obtained by locating therein enzyme structural gene loci that are homologous to Chinese Spring loci with known chromosomal locations. In the strictest sense, the region of homoeology identified is only that occupied by the genes themselves. However, it appears likely that the gene synteny relationships that existed in the ancestral Triticeae genome are largely conserved in the Triticeae genomes that exist today. Chromosome-arm locations may also be largely conserved. Twenty-seven paralogous sets consisting of three enzyme structural gene loci and five sets consisting of two loci have been located in chromosome arms in genomes A, B, and

D in Chinese Spring. Fifteen or more enzyme loci orthologous to Chinese Spring loci have been located in chromosomes or chromosome arms in each of the genomes E, H, R, and S^1. The synteny relationships among the loci studied in genomes A, B, D, H, and S^1 are entirely conserved. A translocation difference between these genomes and genome E is indicated by the chromosomal location of one E-genome locus, which differs from that of orthologous loci in the other genomes. Due to several translocation differences between genome R and genomes A, B, D, E, H, and S^1, the synteny relationships among several R-genome loci differ from those of orthologous loci in the other six genomes. Chromosome-arm locations have been determined for 104 A-, B-, D-, and E-genome loci that are members of homologous sets. These are conserved, with one exception due to the apparent E-genome translocation and one other possible exception involving a B-genome locus. In view of these findings, it is apparent that the identification of members of homologous sets of gene loci in chromosomes of different genomes will usually be indicative of a major region of homoeology.

The ability to identify homoeologous Triticeae chromosomes, chromosome arms, and chromosome segments is important in many basic and applied investigations, including those designed to transfer alien genetic material into cultivated wheats by cytogenetic and molecular methods. At the present time, several paralogous enzyme structural gene sets mark six Chinese Spring homoeologous chromosome groups, but only one is known in group 2 and only one or two in a few chromosome-arm groups. Genetic-map positions have been reported for only nine wheat enzyme loci. Consequently, a high priority in future research should be given to determining the chromosome-arm locations of many more enzyme structural gene loci in several Triticeae genomes and the intrachromosomal genetic-map positions of a large number of loci in a representative group of Triticeae genomes.

5D Genetic and Biochemical Studies of Nonenzymatic Endosperm Proteins

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The endosperm of common wheat (*Triticum aestivum* L.) contains a great number of nonenzymatic storage proteins that are the components of gluten, one of the most intricate naturally occurring protein complexes. Gluten may be subdivided, on the basis of differential solubility, into gliadin and glutenin, as described by Osborne (1907). Gliadin is a fraction, largely monomeric, that is soluble in alcohol-containing solutions. Glutenin consists of numerous polypeptides that are further associated covalently and noncovalently into high-molecular-weight (MW) complexes, which are insoluble in alcohol but may be soluble in solutions containing dilute acids or alkali, denaturants, detergents, or disulfide-reducing agents. In addition, some albumin and globulin proteins normally soluble in water or dilute salt solutions may also be incorporated into gluten during extraction or mixing. Several excellent reviews consider gluten's composition, properties, interrelationships of its constituent proteins, and use in genetic analysis (Kasarda et al., 1976; Miflin and Shewry, 1979; Wall, 1979; Wrigley, 1982; Kasarda et al., 1984a; Konarev et al., 1979; Stegemann and Pietsch, 1983).

Gluten is likely to contain several hundred different polypeptides, many being homologous. This heterogeneity is in part due to gene duplication followed by mutation; it is also due to the hexaploid nature of wheat, which evolved from three separate but related diploid species. Thus, each homoeologous chromosome group contains structural genes having similar positions within each genome. Since few constraints regulate gene expressions, their translated proteins serve as accurate "fingerprints" and can be used to identify genotypes, to provide markers of genes, and to determine genetic and evolutionary relationships.

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Several methods are now extensively used to determine relationships among proteins within a genotype and to differentiate cultivars within a species; these methods may also reveal relationships among species and genera, since mutational rates can be used to predict evolutionary divergence. In wheat breeding, these proteins may provide markers for specific quality characteristics. This review will consider the application of electrophoresis, high-performance liquid chromatography, immunochemical procedures, and protein sequence analysis to wheat genetic studies and improvement through breeding.

5D–1 GEL ELECTROPHORESIS

In gel electrophoresis, proteins migrate in an electric field through a porous matrix, typically composed of polyacrylamide or starch. Mobilities are directly related to charge and inversely related to size; however either size or charge can be suppressed. Thus, in isoelectric focusing, proteins migrate in a pH gradient to positions of electric neutrality that are independent of MW. In sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE), SDS masks protein charge, and thus separations depend only on size. The following sections review the value of gel electrophoresis for wheat cultivar identification and aneuploid analysis, and for determining evolutionary relationships and predicting quality.

5D–1.1 Cultivar Identification

Where wheat is marketed as pure cultivars, cultivar identification may be necessary to determine or assure quality. It also may be desirable to identify genotypes used in breeding programs. Cultivar identification is now possible through electrophoresis of gliadin, glutenin, albumin plus globulin, and total protein extracts.

5D–1.1.1 Gliadins

In 1959, Jones et al. demonstrated that moving-boundary electrophoresis in aluminum lactate-lactic acid buffer, pH 3.2, could resolve gluten into several fractions. Combining this buffer with zone electrophoresis in starch gels (Smithies, 1955) significantly improved gliadin resolution (Elton and Ewart, 1960; Woychik et al., 1961; Elton and Ewart, 1962), permitting cultivar differentiation. Wheat cultivar identification by starch gel electrophoresis (SGE) of gliadins has become a widely used method (Autran and Bourdet, 1975; Wrigley et al., 1982a). (Typical results are shown in Fig. 5D–1.) Twenty to 30 bands are normally revealed by this method; on the basis of their presence, absence, and intensity, keys have been developed for identifying cultivars. Computer-assisted identification also is possible. Gliadins are well suited for cultivar identifi-

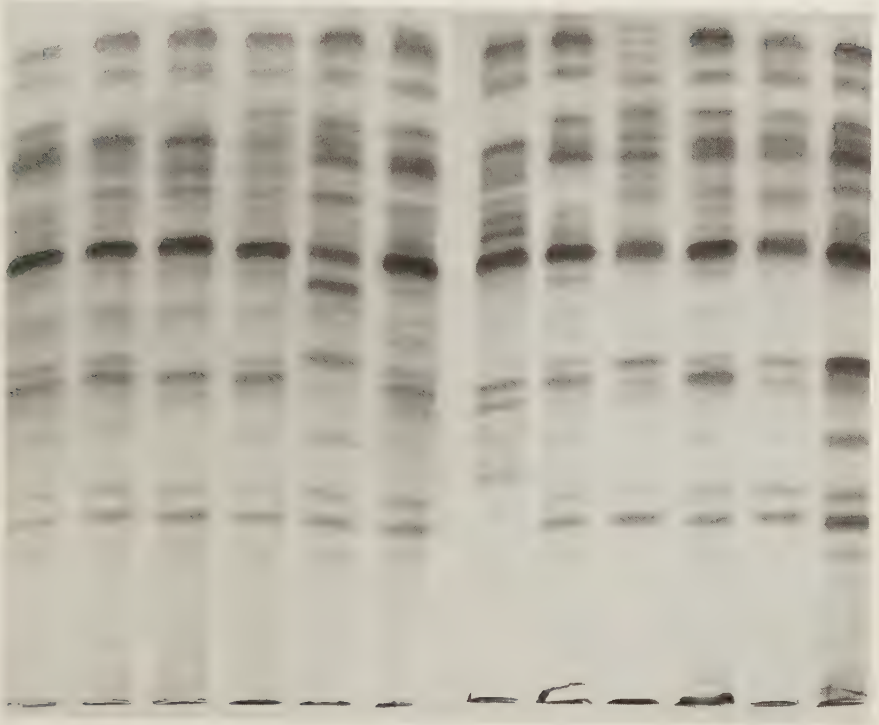

Fig. 5D–1. Starch gel electrophoresis (SGE) patterns of gliadins from the French wheat cultivars (*left to right*) Capitole, Hardi, Champlein, Joss, Etoile de Choisy, Cappelle, Magali, Moisson, Rex, Remois, Florence-Aurore, and Heima. Electrophoretic migration at pH 3.2 was from anode (origin at bottom) to cathode (top). From Autran and Bourdet (1975).

cation because of their heterogeneity, monomeric nature, ease of extraction, stability, and near-constant expression under various environmental conditions. Starch gel electrophoresis of gliadins can be performed on flour samples or on single kernels. Consequently, SGE of gliadins is widely used for cultivar identification.

Starch gel electrophoresis uses simple equipment and a nontoxic support, but resolution may vary and gels are difficult to prepare reproducibly. It is easier to prepare reproducible gels from acrylamide, and PAGE of gliadin is now widely used for wheat cultivar identification (Bushuk and Zillman, 1978; Wrigley et al., 1982a). (An example is shown in Fig. 5D–2.) Separations are analogous to those obtained by SGE, but resolution is generally better. Several excellent alternative PAGE procedures have been proposed (Tkachuk and Mellish, 1980; Lookhart et al., 1982; Khan 1982; Khan et al., 1983). Most separations are performed in aluminum lactate buffer at acidic pH, but good resolution can also be obtained using acetic acid/glycine buffer (Maier and Wagner, 1980). Alkaline

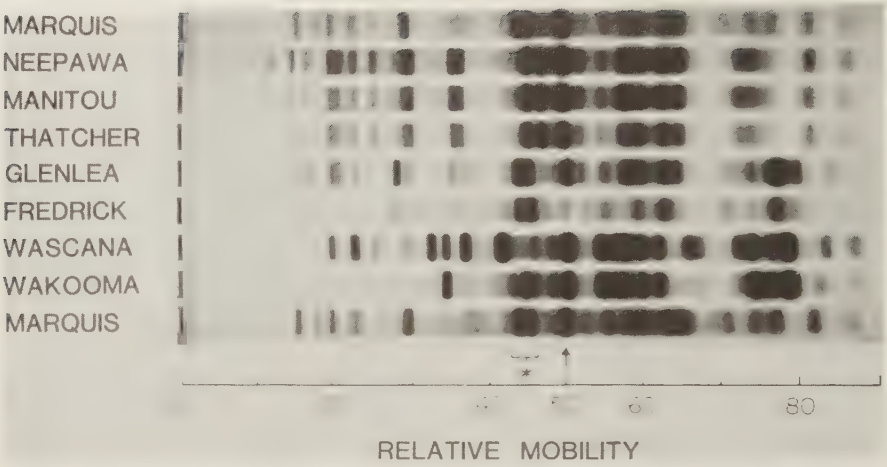

Fig. 5D–2. Polyacrylamide gel electrophoresis (PAGE) patterns of gliadins from nine wheat cultivars. From Bushuk and Zillman (1978).

buffers (Hussein et al., 1977; Hussein and Stegemann, 1978; Ohms, 1980b), though used less frequently, also may give good separations; in particular, acidic and alkaline buffers may be effectively combined in a two-dimensional horizontal PAGE procedure (Mecham et al., 1978), in which samples for alkaline PAGE are loaded in the middle of the gel to prevent cathodic components from being lost.

Gradient gel electrophoresis of gliadins also permits cultivar identification. In this procedure, gel concentration increases with migration distance, mobilities decrease, and zones are sharpened (du Cros and Wrigley, 1979; Wrigley et al., 1982a) (Fig. 4D–3). Advantages of the method include speed, convenience, and commercial availability of gels; reproducible homemade gels may be somewhat difficult to prepare.

Isoelectric focusing (IEF), first applied to gliadin by Wrigley (1968), also differentiates wheat cultivars (du Cros and Wrigley, 1979; Wrigley et al., 1982a). Isoelectric focusing separations, which depend only on charge, thus complement other electrophoresis procedures; however, the cost of carrier ampholytes may restrict routine use of IEF.

SDS-PAGE of gliadin may also be useful for cultivar identification (Shewry et al. 1978). SDS-PAGE complements SGE, and may differentiate some cultivars that appear identical by SGE.

Two-dimensional procedures provide the best available electrophoretic resolution of gliadin. Nearly any two procedures may be combined, but most separations use either IEF followed by SGE (Wrigley, 1970; Wrigley and Shepherd, 1973; du Cros and Wrigley, 1979) or PAGE at two pHs (Mecham et al., 1978). Usually 40 to 50 gliadins resolve, far more than in any one-dimensional method, and thus two-dimensional methods may be able to identify cultivars that appear identical in one-dimensional procedures. Two-dimensional electrophoresis is perhaps too complex for routine use, but is invaluable for special applications.

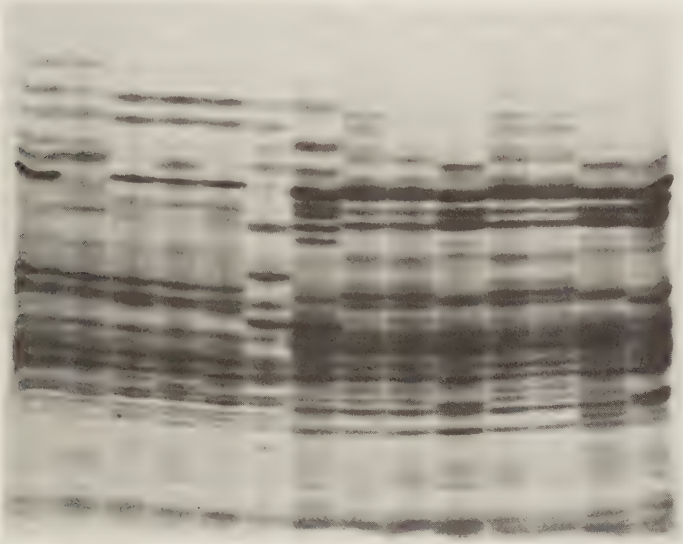

Fig. 5D–3. Gradient gel electrophoresis in sodium lactate of endosperm proteins from six wheat cultivars (*left to right*: Emblem, Stockade, Oxley, Kewell, Condor, and Halberd) and from eight triticale lines under consideration for release in Australia. Gel concentration ranged from 3% at top of gel (origin) to 27%. From du Cros and Wrigley (1979).

5D–1.1.2 Glutenin

Wheat cultivar identification by electrophoresis of glutenin is less common than by electrophoresis of gliadin. In part, this is because glutenin must be converted to its subunits before electrophoresis, through reduction of disulfide bonds in the presence of either strong denaturants (e.g., 8 *M* urea) or detergents (e.g., SDS). Resulting subunits can be classified as being high-MW (ethanol-insoluble) or low-MW (ethanol-soluble). Also, glutenin's subunits may be difficult to separate because of their high MWs, solubilities, and associative tendencies. Nevertheless, coding of many high-MW glutenin polypeptides is different from that of most gliadins, and glutenin subunit compositions are nearly constant for any cultivar. Thus, if gliadin electrophoresis does not differentiate genotypes, analysis of glutenin subunits may succeed.

Differences in glutenin subunit composition clearly exist among cultivars (Elton and Ewart, 1966; Huebner, 1970). Resolution of glutenin subunits by SGE is relatively poor, however, and their isolation is difficult. The application of SDS-PAGE (Bietz and Wall, 1972) permitted glutenin subunits to be more easily characterized. Nevertheless, resolution originally was not sufficient to differentiate most cultivars: subunit compositions of glutenins isolated from single hexaploid wheat kernels for 75 out of 80 cultivars were similar (Bietz et al., 1975). Five cultivars, however, including 'Nap Hal', differed markedly in high-MW (100 000–130 000 daltons) subunit composition. Because they have a much higher

MW than all other wheat polypeptides, high-MW glutenin subunits in easily obtained total protein extracts also can be analyzed by SDS-PAGE.

By application of higher resolution SDS-PAGE, considerably more variability has been observed among high-MW glutenin subunits (Payne et al., 1981b) (Fig. 5D–4.) Similar studies have been performed by Lawrence and Shepherd (1980) and by Galili and Feldman (1983b). At least 20 distinct high-MW subunits have been identified in wheat. Generally, four to five high-MW subunits are present in any cultivar; polymorphism among these subunits, arising from expression of different alleles, permits cultivar identification (du Cros et al., 1980; Wrigley et al., 1982a). These differences are also apparent in total protein extracts, simplifying sample preparation. Thus, SDS-PAGE of high-MW glutenin subunits may be useful for cultivar identification, particularly when cultivars have similar gliadin compositions.

5D–1.1.3 Albumins and Globulins

Electrophoresis of albumins and globulins may also be useful in wheat cultivar differentiation, particularly if gliadin and glutenin subunits are

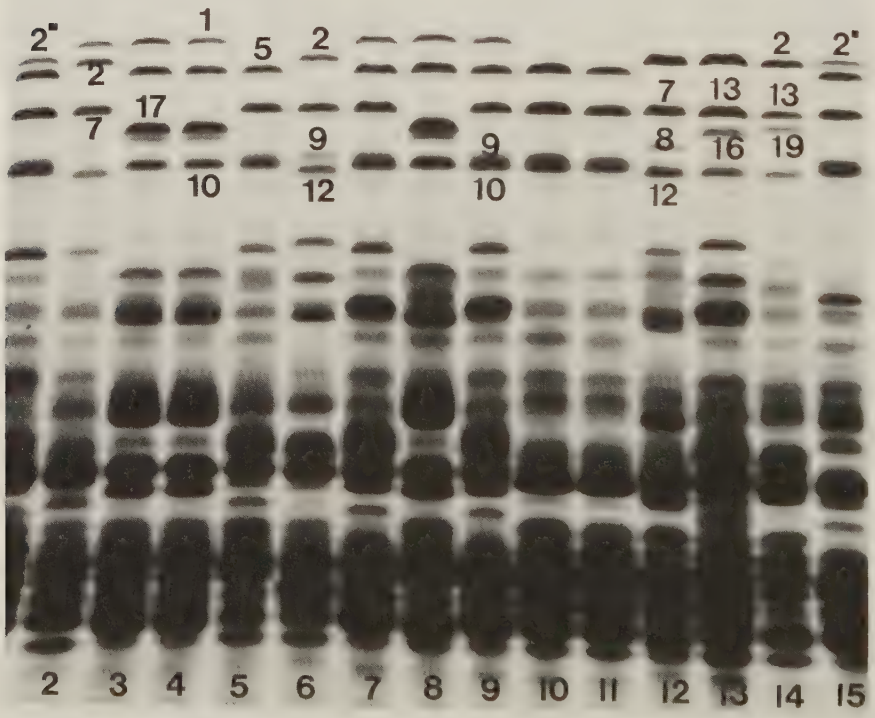

Fig. 5D–4. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) using a 10% gel of flour proteins from 15 cultivars of bread wheat. Numbers on gel indicate high-molecular-weight (82 000–125 000 apparent molecular weight) glutenin subunits exhibiting major compositional variation. From Payne et al. (1981b).

similar, because albumins and globulins are coded by different chromosomal loci. Elton and Ewart (1964) showed significant qualitative and quantitative differences among albumins of several wheat cultivars by SGE. Doekes (1968) examined 80 wheat cultivars by SGE and densitometry, dividing them into five subgroups reflecting genetic relationships. Ohms (1980b) demonstrated that PAGE of albumins and globulins extracted in the presence of 2-mercaptoethanol could also differentiate some genotypes. A similar procedure was reviewed by Wrigley et al. (1982a), who noted, as did Johnson (1972), that electrophoresis of soluble proteins may be more useful for comparisons of species than of cultivars.

5D-1.1.4 Total Proteins

SDS-PAGE patterns of total protein extracts can also differentiate wheat cultivars (Fullington et al., 1980); both qualitative and quantitative differences exist between genotypes. Galili and Feldman (1983b) also used high-resolution SDS-PAGE to compare wheats (Fig.5D–5.) Much qual-

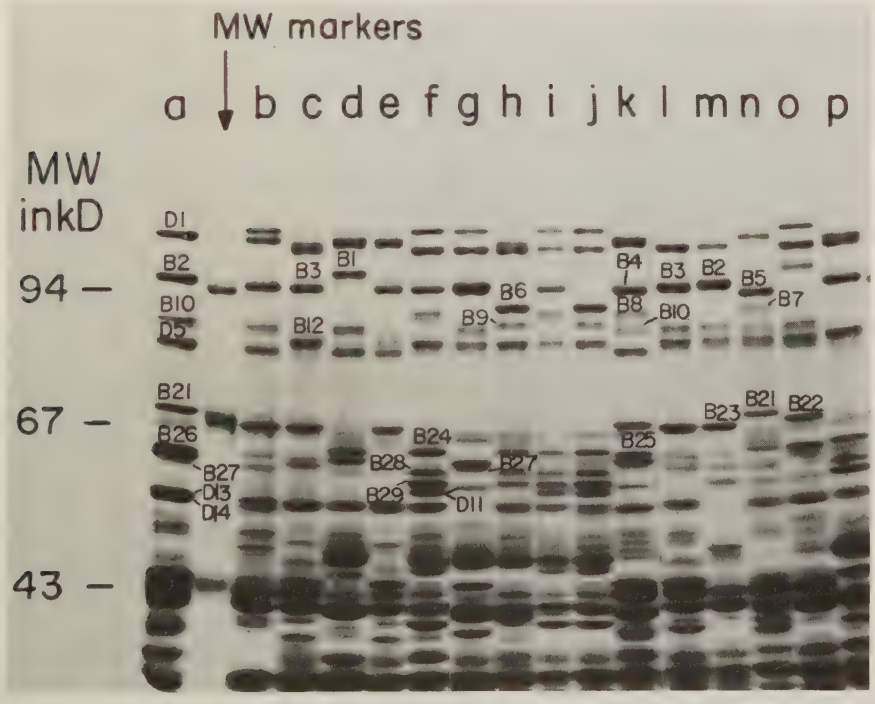

Fig. 5D–5. High-resolution sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) of total protein extracts from the hexaploid wheat cultivars (a) Chinese Spring, (b) Merav, (c) Florence Aurore, (d) Ribeiro, (e) Lackish, (f) Miriam, (g) Jaral, (h) Tanori, (i) Inia 66, (j) Sonora 66, (k) TAA19, (l) Hazera 112, (m) Hazera 776, (n) Mabrouk, (o) Selkirk, and (p) WA 6389. Known molecular weight (MW) markers were fractionated in a parallel lane, with apparent MW indicated on the left. Specific polypeptides are identified within the gel. From Galili and Feldman (1983b).

itative and quantitative variation was observed both in high-MW subunits (glutenin) and in lower-MW subunits. Clearly, this may be a valid alternative to other electrophoretic procedures for cultivar identification.

5D–1.2 Locations of Genes Coding Gluten Proteins

The heterogeneity of wheat protein complicates many studies, but it may also be used advantageously in genetic studies. Determination of chromosomal control may clarify synthesis, interrelationships, and expression of proteins; such proteins may then be used as markers (either causative or closely linked) of desirable or undesirable characteristics in breeding. Such an application is possible largely because of the availability of wheat aneuploids pioneered in 'Chinese Spring' by E.R. Sears (1954), and because of high-resolution electrophoretic methods. Others have recently reviewed genetic analyses of wheat proteins by electrophoresis (Wrigley, 1982; García-Olmedo et al., 1982; Porceddu et al., 1983; Payne et al., 1984b); this section will focus on some of the landmark studies in this area.

5D–1.2.1 Gliadins

In one of the first uses of electrophoresis to characterize wheat aneuploids, Boyd and Lee (1967) noted changes in gliadin SGE patterns of ditelocentric vs. euploid lines of Chinese Spring; when one and the same arm of each of the 1D chromosome pair was removed, two slow-moving ω-gliadins disappeared, showing that they represent heritable characteristics. Shepherd (1968) subsequently examined all nullisomic-tetrasomic and ditelocentric Chinese Spring lines: 9 of 17 major bands were accounted for by the absence of genes on the short arms of chromosomes 1A, 1B, 1D, 6A, and 6D; chromosome dosage effects observed for other bands suggested that one-dimensional SGE does not resolve all gliadins, since some bands were coded for by multiple genes on different chromosome arms. Wrigley and Shepherd (1973) combined IEF with SGE in a two-dimensional procedure, and resolved Chinese Spring gliadins into 46 components, most coded by genes on chromosome groups 1 and 6 (Fig. 5D–6). Other high-resolution, two-dimensional electrophoretic methods may also demonstrate chromosomal control: Mecham et al. (1978) used PAGE first at pH 3.2 and then at pH 9.2 to separate gliadins. Brown et al. (1979) combined IEF with SDS-PAGE to obtain high-resolution separations. In a variation of this method, Jackson et al. (1983) and Payne et al. (1984b) combined separations by both IEF and non-equilibrium pH-gradient electrophoresis (NEPHGE) in the first dimension with SDS-PAGE in the second (Fig. 5D–7), giving the highest-resolution electrophoretic separations of wheat endosperm proteins obtained to date. These studies conclusively demonstrate that genes coding most α and β gliadins are on the short arms of homoeologous group 6 chromosomes, whereas most ω- and γ-gliadin genes are on the short arms of chromosomes 1A, 1B, and 1D.

Fig. 5D–6. Two-dimensional electrophoretic protein map of gliadins of the wheat cultivar Chinese Spring showing identity of chromosomes controlling synthesis of specific components. From Wrigley and Shepherd (1973).

Electrophoretic analysis of gliadins from aneuploids has revealed considerable additional genetic information. One of the most significant concepts is that gliadins are inherited as blocks of components, suggesting that gliadin genes are clustered in discrete loci, each of which may vary in composition (Sozinov and Poperelya, 1980). Each group 1 and 6 chromosome has only one complex locus, so that loci are inherited independently, causing variation that permits cultivar differentiation; this independent inheritance has led to a proposed nomenclature based on gliadin blocks. Mecham et al. (1978) and Branlard (1983) have also observed that blocks of closely linked genes code for gliadin proteins.

Although most original genetic studies of gliadins were done in Chinese Spring, various substitution lines also permit analysis of other hexaploid cultivars (Mecham et al., 1978; Brown et al., 1981; Kasarda et al., 1984a). These studies confirm the groups 1 and 6 coding observed in Chinese Spring. Similarly, durum (*Triticum turgidum* L.) D-genome disomic-substitution lines, each having a different D-genome chromosome pair substituted for homoeologous A- or B-genome chromosomes, have made possible chromosomal location of genes for most durum gliadins resolved by one- or two-dimensional electrophoresis (Joppa et al., 1983b; du Cros et al., 1983).

5D–1.2.2 Glutenins

Because of their higher MWs, associative tendencies, and poor solubilities, glutenin subunits may separate poorly upon SGE or PAGE. It

was only through SDS-PAGE (Bietz and Wall, 1972) that high-MW glutenin subunits were found to be coded by genes on the long arms of chromosomes 1D and 1B (Orth and Bushuk, 1974; Bietz et al., 1975). Because these subunits are unique to glutenin and because chromosomes 1B and 1D have been associated with bread wheat quality (Welsh and Hehn, 1964; Morris et al., 1966), Bietz et al. (1975) examined numerous hexaploid cultivars: some variability among high-MW subunits was noted, but most cultivars appeared similar. These results were subsequently extended (Payne et al., 1980; Lawrence and Shepherd, 1981b; Galili and Feldman, 1983a), using higher resolution SDS-PAGE. Additional heterogeneity became apparent among cultivars, and high-MW glutenin subunits were found to be inherited in blocks, as are gliadins, and to be controlled by presumably homologous gene loci on the long arms of chromosomes 1A, 1B, and 1D (Lawrence and Shepherd, 1981a; Payne et al., 1982; Galili and Feldman, 1983b). Crosses between wheats having different high-MW glutenin subunit compositions have revealed at least 21 allelic variants at glutenin subunit loci *Glu-A1*, *Glu-B1*, and *Glu-D1* (Payne et al. 1984b). Glutenin subunit inheritance in F_1 and F_2 generations is co-dominant (Burnouf et al., 1981; Burnouf et al., 1983b), so subunits are expressed whatever their gene dosage in the endosperm. As discussed below, specific alleles are associated with bread-making quality (Burnouf and Bouriquet, 1980; Payne et al., 1980), permitting screening of early generation progeny for desirable characteristics.

Glutenin's ethanol-soluble low-MW subunits (Bietz and Wall, 1980) have recently been shown to be coded by genes on the short arms of chromosomes 1A, 1B, and 1D (Jackson et al., 1983). These polypeptides may be of considerable importance, since in durum wheat the presence or absence of a low-MW glutenin subunit is as closely related to pasta quality as are the more commonly used gliadin marker protein bands 42 and 45 (Payne et al., 1984c).

Although allelic variation among glutenin subunits is frequently apparent by one-dimensional SDS-PAGE, two-dimensional separations provide additional information. In characterizing glutenin, Brown et al. (1979, 1981) and Brown and Flavell (1981) used combined IEF and SDS-PAGE, and Jackson et al. (1983) and Payne et al. (1984b) also used nonequilibrium pH-gradient electrophoresis (see Fig. 5D–7). These techniques are powerful tools for selection and improvement of wheat lines.

5D–1.3 Use of Electrophoresis to Study Genetic Relationships Among Genera and Species

Early studies using protein electrophoresis to assess phylogenetic affinities among wheat genera and species were performed by B.L. Johnson and co-workers. Proteins may provide a more direct measure of gene homology than morphological relationships (Johnson and Hall, 1965).

Fig. 5D–7. Two-dimensional gel electrophoretic fractionation of total endosperm proteins of the wheat cultivar Chinese Spring using two separate first-dimension separations (isoelectric focusing [*i.e.f.*]) and nonequilibrium pH-gradient electrophoresis [*n.e.p.h.g.e.*], and sodium dodecyl sulfate-polyacrylamide gel electrophoresis [*SDS p.a.g.e.*] in the second dimension. Abbreviations used: *h.m.m.*, high molecular mass; *l.m.m.*, low molecular mass. From Payne et al. (1984b).

As gene mutations accumulate within a species, charges of proteins also may change, affecting their mobilities. Since polyploid genomes represent gene systems transmitted relatively intact from donor species, protein spectra should indicate genome donors, as well as homologies. Johnson (1972) thus analyzed gliadin or albumin proteins by PAGE combined with densitometry, and determined correlation coefficients between corresponding spectral points to estimate genetic relationships. His conclusions generally agreed with other data, while suggesting novel relationships. In addition, comparison of triticale (X *Triticosecale* Wittmack) with wheat and rye (*Secale* spp.) confirmed that electrophoretic spectra of amphiploids are the sum of spectra of parental proteins.

Considerable care, however, must be used in such comparisons. For example, intraspecific variability in gliadin composition may be as great as interspecific variation (Boyd et al., 1969); an obvious example is variability among *T. aestivum* gliadins, which permits cultivar identification. However, generally there is little intraspecific variation among albumins, making them more useful than gliadins for comparing species (Wrigley

et al., 1982a). In crosses between known parents, however, gliadins also provide suitable markers. A few examples of such methods will be noted.

Studies of wheat and rye have shown that characteristic markers exist for specific *Triticum* and *Secale* chromosomes (Shepherd and Jennings, 1971), and that triticale's proteins are simply inherited from its parents (Chen and Bushuk, 1970). This permits, for example, electrophoretic determination of amounts of wheat and rye in a mixture (McCausland and Wrigley, 1976). Similarly, electrophoretic analysis of proteins characteristic of the D genome of *T. aestivum* permits determination of amounts of common wheat in pasta products (Feillet and Kobrehel, 1972). Differential staining of albumins and globulins may also help to reveal evolutionary relationships and pedigrees of species and genera (Caldwell and Kasarda, 1978). SDS-PAGE is also useful to demonstrate and clarify evolutionary relationships in the Triticinae (Preston et al. 1975), and to reveal marker proteins characteristic of specific chromosomes in barley (*Hordeum* spp.), rye, *Triticum umbellulatum*, and *Agropyron elongatum* (Lawrence and Shepherd, 1981a). SDS-PAGE of total protein extracts, in combination with densitometry, may also reveal relationships among diploid and polyploid *Triticum* (including *Aegilops*) spp. (Cole et al., 1981). Thus, there are numerous ways to use electrophoresis of seed proteins to mark genetic systems and to define genotypes (Konarev et al., 1979).

5D–1.4 Predication of Wheat Quality by Electrophoresis

To a large degree, the functional and nutritional qualities of wheat are related to its proteins. Since all protein fractions are extremely heterogeneous, high-resolution techniques such as electrophoresis may yield much qualitative and quantitative information, and it is likely that such data may be related to quality. Such relationships already have been found and are likely to increase (see Wrigley, 1982, and Khan, 1982, for reviews). This section will review recent results of relating electrophoresis to wheat quality.

Damidaux et al. (1978) first noted a consistent relationship between two durum gliadins, bands 45 and 42, and gluten viscoelasticity (Fig. 5D–8). Cultivars having gliadin 45 typically have cooking quality superior to cultivars with gliadin 42. These results were confirmed by Kosmolak et al. (1980). Gliadins 42 and 45 were found to be coded by two codominant alleles of a single gene on chromosome 1B (Damidaux et al. 1980). Computer-based pattern analysis could also demonstrate relationships of gliadin electrophoregrams to dough strength and weakness (du Cros et al., 1982). In addition, improved resolution of two-dimensional electrophoresis accentuated the heterogeneity of these proteins (du Cros et al., 1983). Thus, electrophoresis can be valuable in screening for grain quality. It is important to realize, however, that observed associations may be due to close proximity of genes coding gluten-protein markers to other genes that confer quality, and not to any direct contribution of specific poly-

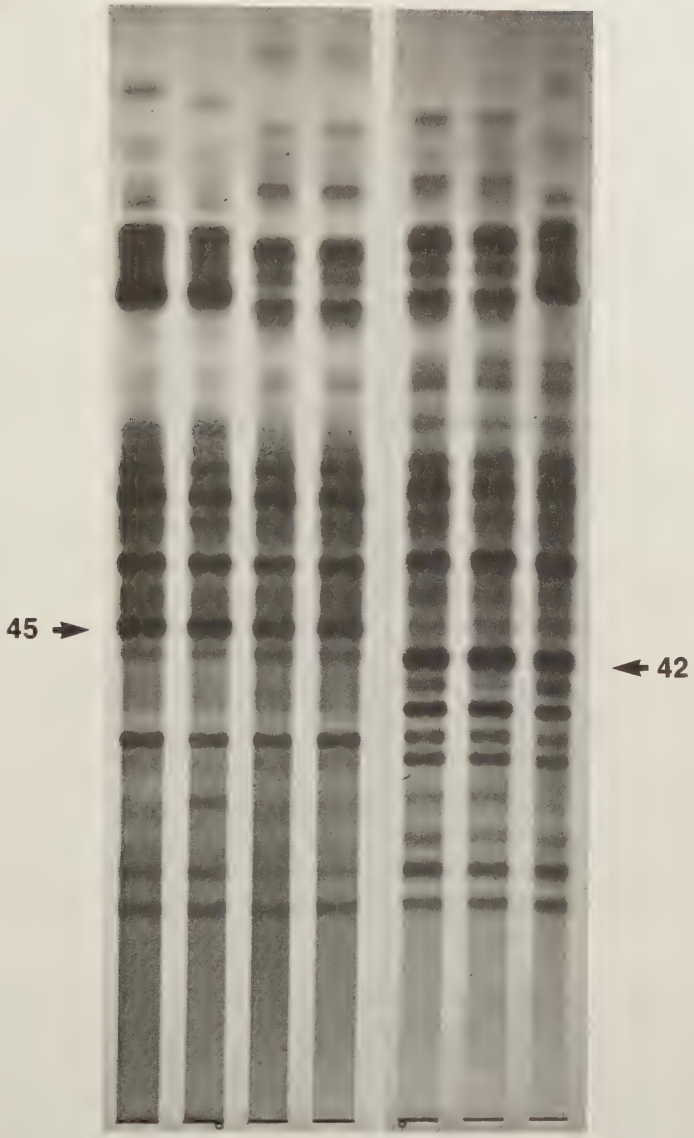

Fig. 5D–8. Polyacrylamide gel electrophoresis (PAGE) of gliadins from seven cultivars of durum wheat. Cultivars on the left (D 71-75, Cocorit 71, Blondur, and Valdur) have band 45 associated with strong gluten viscoelasticity, and cultivars on the right (Wells, Lakota, and Durtal) have band 42, associated with weak gluten properties. From Damidaux et al. (1978).

peptides to quality (Wrigley, 1982). For example, an intermediate-MW durum-glutenin subunit (Autran, 1981) is more closely associated with cooking quality than are the gliadin marker proteins 45 and 42 (Payne et al., 1984c).

Much evidence now suggests that hexaploid-wheat protein fractions may also be related to bread-making quality. For example, blocks of genes that code gliadin proteins may be related to characteristics such as sedimentation volume (Sozinov and Poperelya 1980). Furthermore, there are significant correlations between specific gliadin electrophoretic bands and characteristics such as hardness and dough strength (Branlard and Rousset, 1980; Wrigley et al., 1981, 1982b, 1982c; Pogna et al., 1982). Detection of such relationships is greatly facilitated through the use of computers. As noted above, however, such correlations do not necessarily indicate cause and effect, but rather may be due to close linkage of gliadin genes to other genes actually associated with quality, or to a relationship of electrophoretic pattern to pedigree (which in turn may relate to quality). Other proteins also may be associated with good baking quality: for example, two proteins extracted by Tris-glycine buffer, pH 8.9, in the presence of 2-mercaptoethanol occur preferentially in cultivars with good baking quality (Ohms, 1980a).

One of the most intriguing correlations between protein composition (as revealed by electrophoresis) and bread-making quality concerns glutenin, the strength protein of wheat. Payne et al. (1979, 1981a) identified specific high-MW glutenin subunits that correlated with quality; similar results were obtained by Burnouf and Bouriquet (1980) and by Moonen et al. (1982). Much allelic variation exists at the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci (Fig. 5D–9), and variants differ in their relationship to quality. These studies are currently useful in directing breeding strategies, and increased knowledge of sequences of these subunits may soon reveal the true relationship between glutenin structure and functionality (Shewry et al., 1984).

5D–2 HIGH PERFORMANCE LIQUID CHROMATOGRAPHY (HPLC)

In liquid chromatography, solutes dissolved in a flowing-liquid mobile phase pass through columns packed with solid supports; separations are based on relative interactions of solutes with column packings. Column techniques have provided good separations of wheat proteins based upon ionic interactions between solutes and support (ion-exchange chromatography) or upon solute penetration into or exclusion from a porous matrix (size-exclusion chromatography). More recently, hydrophobic interaction chromatography, based upon bonding between nonpolar amino acids on protein surfaces with solid hydrophobic supports, also has been applied to wheat proteins (Popineau and Godon, 1978; Caldwell, 1979; Chung and Pomeranz, 1979). These separations, however, frequently do not adequately resolve complex mixtures and may not separate homologous proteins of similar size and charge. High-performance liquid chromatography (HPLC) overcomes these deficiencies by providing powerful new separation methods. Particularly relevant to proteins are the more

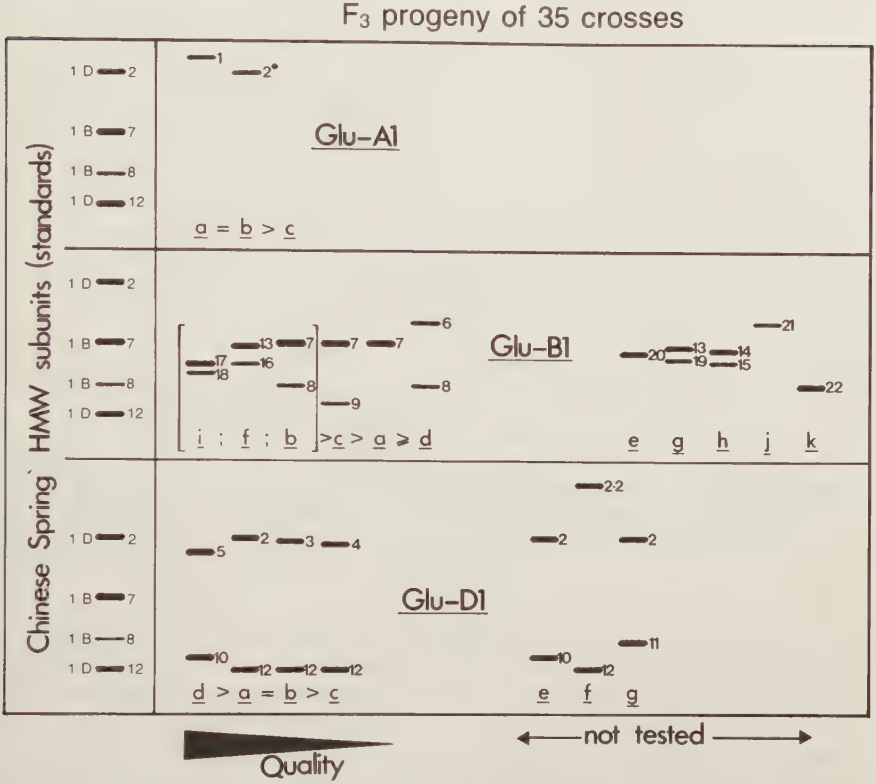

Fig. 5D–9. Allelic variation in high-molecular-weight (HMW) subunits of wheat glutenin and their relationship to breadmaking quality. Standard HMW subunits of Chinese Spring coded by genes on chromosomes 1A, 1B and 1D (the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci) are indicated on the left. Letters *a-k* designate each allelic group. Subunits more strongly associated with good quality are on the left. From Payne et al. (1984b).

porous (typically ≥300 Å) silica-based columns (Regnier and Gooding, 1980; Hearn et al., 1982; Wehr, 1984). The HPLC technology is now being applied extensively to wheat proteins; this section will briefly review the methods and their advantages, show some typical separations, and give examples of applications of HPLC to analysis of wheat gluten proteins.

5D–2.1 Reversed-Phase HPLC

High-resolution HPLC separations of cereal proteins were first obtained by Bietz (1983, 1985). A typical chromatogram of wheat gliadin is presented in Fig. 5D–10. Such a separation can easily be obtained, using any system with gradient capabilities that is equipped with one of the many available large-pore silica-based columns recommended for

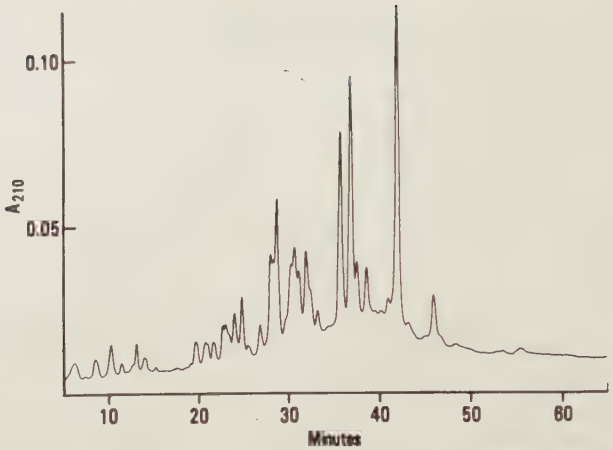

Fig. 5D–10. Reversed-phase high-performance liquid chromatography (RP-HPLC) of gliadin proteins (cv. Centurk) extracted from a single wheat kernel with 70% ethanol and analyzed at 70 °C on a SynChropak RP-P (C_{18}) column 4.1 × 250 mm), using a gradient from 28 to 50% acetonitrile in the presence of 0.1% trifluoroacetic acid during 55 min, and detection by absorbance (A) at 210 nm.

proteins. In reversed-phase (RP) HPLC, proteins interact hydrophobically with a nonpolar phase covalently attached to uniform porous silica. Initial RP-HPLC conditions are relatively hydrophilic, so that all proteins bind to the column; subsequently, the nonpolar nature of the solvent progressively increases, and proteins selectively elute in order of increasing hydrophobicity. The solvent system most useful for most proteins includes water, acetonitrile, and 0.1% trifluoroacetic acid; relatively nonpolar solvents may be especially useful for hydrophobic wheat proteins. Recent studies in our laboratory also have shown improved resolution at increased temperatures, perhaps because association of gluten proteins is minimized (Bietz and Cobb, 1985).

Excellent resolution is easily obtained by RP-HPLC for complex and heterogeneous mixtures. The total number of gliadins resolved (Fig 5D–10), for example, equals or exceeds resolution by most other methods, including two-dimensional electrophoresis. Electrophoretic analysis of single RP-HPLC peaks generally reveals highly purified proteins (Bietz, 1983; Burnouf and Bietz, 1984a; Huebner and Bietz, 1984); however, multiple components sometimes occur in single peaks, emphasizing wheat protein heterogeneity. Since RP-HPLC separates proteins by surface hydrophobicity, it complements chromatographic and electrophoretic procedures based on size or charge, thereby providing a powerful new tool for protein isolation, characterization, and comparison.

RP-HPLC has numerous other advantages. First of all, it is fast: optimal resolution requires about one hour with present technology, and considerably faster separations are possible. Run-to-run reproducibility is excellent; column-to-column reproducibility also is good, and columns are very stable. Good recovery of proteins from columns is achieved.

Proteins may be detected by absorbance of peptide bonds at 210 nm, making RP-HPLC extremely sensitive; half kernels can easily be analyzed, making the procedure nondestructive of germplasm. Alternatively, RP-HPLC is an excellent preparative method for gluten proteins (Bietz, 1983; Burnouf and Bietz, 1984a; Huebner and Bietz, 1984). The HPLC provides accurate quantitative data that are amenable to computer-assisted processing, replotting, and comparison. The RP-HPLC gives excellent separations of albumins and globulins (Bietz, 1983) and of glutenin subunits (Bietz, 1983; Burnouf and Bietz, 1984b) as well as of gliadin, making it suitable for all wheat polypeptides.

5D-2.1.1 Cultivar Identification

The RP-HPLC has already been used in numerous practical applications for wheat-protein analysis. One such application involves identification of wheat cultivars. Since gliadins are accurate genotypic indicators and since RP-HPLC resolves them at least as well as does one-dimensional electrophoresis, RP-HPLC can readily differentiate most wheat cultivars (Bietz, 1983). After optimal conditions for gliadin extraction for RP-HPLC were established (Bietz et al., 1984a), the method was applied to analysis of cultivars from all wheat classes (Fig. 5D–11) (Burnouf et al., 1983a; Bietz et al., 1984b). Most hard red spring wheats, as well as cultivars of other classes, could be readily differentiated by qualitative and quantitative differences among peaks. Cultivars with very similar pedigrees, such as Era and Solar, give similar patterns as observed by electrophoresis. However, because of improved resolution, complementary separations, and better quantitation, RP-HPLC may differentiate some cultivars that by electrophoresis appear identical. If chromosomal loci for gliadins are identical, RP-HPLC may still differentiate cultivars by their glutenin subunits (Burnouf and Bietz, 1984b) or albumin and globulin proteins. Thus, RP-HPLC can identify most wheat cultivars, and it may have certain advantages as compared to electrophoresis. For example, results for any sample are obtained in 1 to 2 h, rather than 1 to 2 days. Even though an operator can analyze fewer samples per day by RP-HPLC than by electrophoresis, recent studies (Bietz and Cobb, 1985), show that increased flow rates and temperatures, and rapid gradients, permit differentiation of most cultivars in only 10 to 15 min, with relatively minor loss of resolution.

RP-HPLC also is useful as a selection tool. For example, it can easily select atypical genotypes in 'Nap Hal' (Bietz et al., 1984b); this cultivar is a source of high-protein and high-lysine genes in breeding improved hard red winter wheat (Johnson et al., 1972). Similarly, genetic purity of cultivars may be established by RP-HPLC, and standard patterns can be defined for registration of genotypes.

5D-2.1.2 Prediction of Quality by RP-HPLC

As described above, numerous proteins related to wheat quality can be analyzed by electrophoresis. Because the resolution of RP-HPLC is

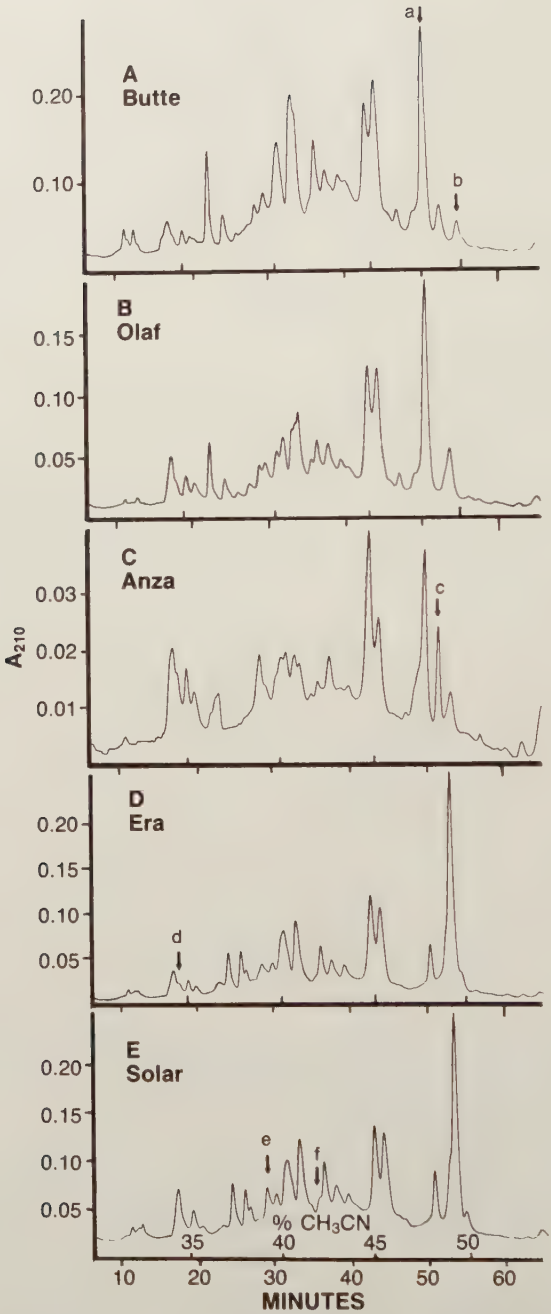

Fig. 5D–11. Differentiation of the hard red spring wheat cultivars (*A*) Butte, (*B*) Olaf, (*C*) Anza, (*D*) Era, and (*E*) Solar by reversed-phase high-performance liquid chromatography (RP-HPLC) of extracted gliadins. From Bietz et al. (1984b).

superior to that of many electrophoretic procedures, it also may reveal such relationships. This has already been confirmed in two separate instances, as follows.

Durum wheat gliadins give characteristic patterns by RP-HPLC, permitting cultivar identification and differentiation (Bietz et al., 1984b) (Fig. 5D–12). All cultivars examined had either peaks *b* to *e* (Fig. 5D–12A) or *i* to *j* (Fig. 5D–12C). This division of cultivars was identical to that based on electrophoretic bands 45 and 42, which predict gluten strength and weakness, respectively. Burnouf and Bietz (1984a) demonstrated that peak *b* corresponds to band 42, and peak *i* to band 45; they also used preparative RP-HPLC to isolate these proteins for further characterization and developed a rapid automated procedure (200 analyses per day) for screening durum quality during early stages of breeding.

High-MW glutenin subunits of hexaploid wheat related to bread-making quality (see previous discussion in this section) also may be analyzed by RP-HPLC. Using optimal conditions for reduction, alkylation, and RP-HPLC analysis of glutenin (Burnouf and Bietz, 1984b), high-MW subunits elute before those of lower MWs; differences among these subunits (Fig. 5D–13B, peaks *c* and *e*) permit cultivar identification. Thus, since these peaks represent subunits that contribute in various degrees to bread-making quality, RP-HPLC can be used (as electrophoresis is used) to predict wheat quality.

RP-HPLC may become valuable for relating polypeptide compositions to technological quality in all types of wheat. Computer analysis of RP-HPLC data also may be useful for analysis of such factors and for identification of additional relationships of quality and protein.

5D–2.1.3 Use of RP-HPLC in Studies of Wheat Aneuploids

As noted above, electrophoresis, which permits locating genes that code specific polypeptides, is a valuable method for breeding and selection. RP-HPLC also can determine chromosomal control of proteins through aneuploid analysis (Bietz, 1983); for example, gliadins coded by genes on missing chromosome arms of Chinese Spring aneuploids can be easily identified, permitting their use as chromosome markers (see Fig. 6 of Bietz et al., 1984b). These studies, along with analyses of 'Cheyenne'/Chinese Spring substitution lines and durum aneuploids, have been described elsewhere by Bietz and Burnouf (1985).

Locations of genes for glutenin subunits likewise can be demonstrated by RP-HPLC aneuploid analyses (Fig. 5D–14). For example, these results show that peaks *a* and *b* are coded by genes on chromosome 1D, and *c* and *d* by genes on the long arm of chromosome 1B. These peaks represent high-MW subunits correlated with quality (Fig. 5D–13), so their analysis by RP-HPLC may be valuable in breeding. A detailed study of glutenin subunit composition in Chinese Spring and in durum aneuploid lines has been completed, permitting assignment of most RP-HPLC peaks to specific chromosome arms (Burnouf and Bietz, 1985). In addition, RP-

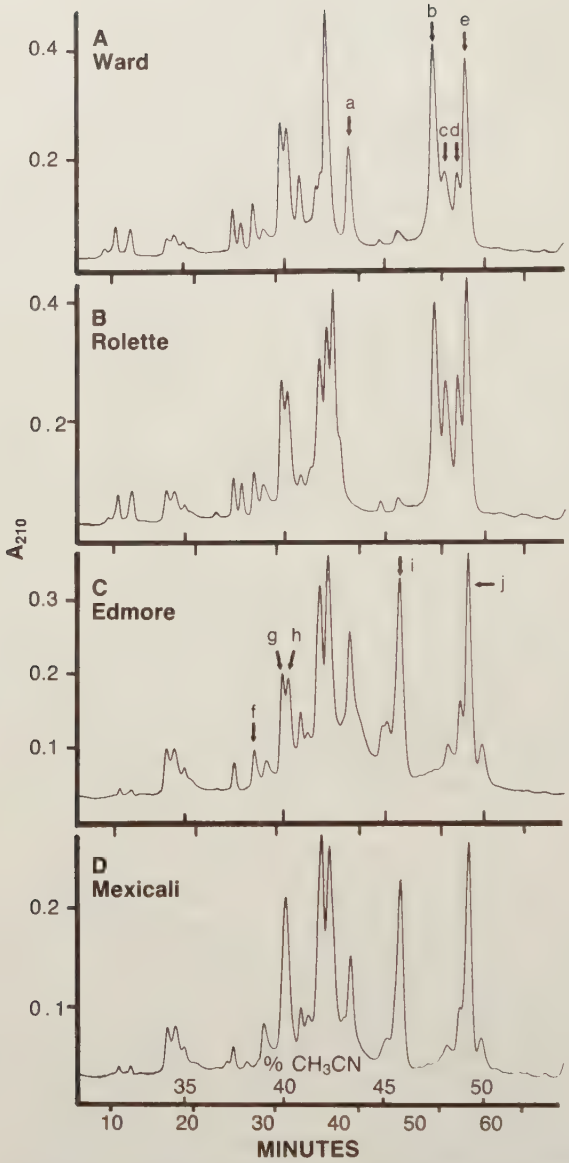

Fig. 5D–12. Differentiation of the durum wheat cultivars (*A*) Ward, (*B*) Rolette, (*C*) Edmore, and (*D*) Mexicali by reversed-phase high-performance liquid chromatography (RP-HPLC) of extracted gliadins. From Bietz et al. (1984b).

HPLC has revealed significant differences among gliadins and glutenins of diploid, tetraploid, and hexaploid *Triticum* spp. and related genera, showing that the method is useful for the study of genetic and evolutionary relationships (Burnouf and Bietz, 1984c).

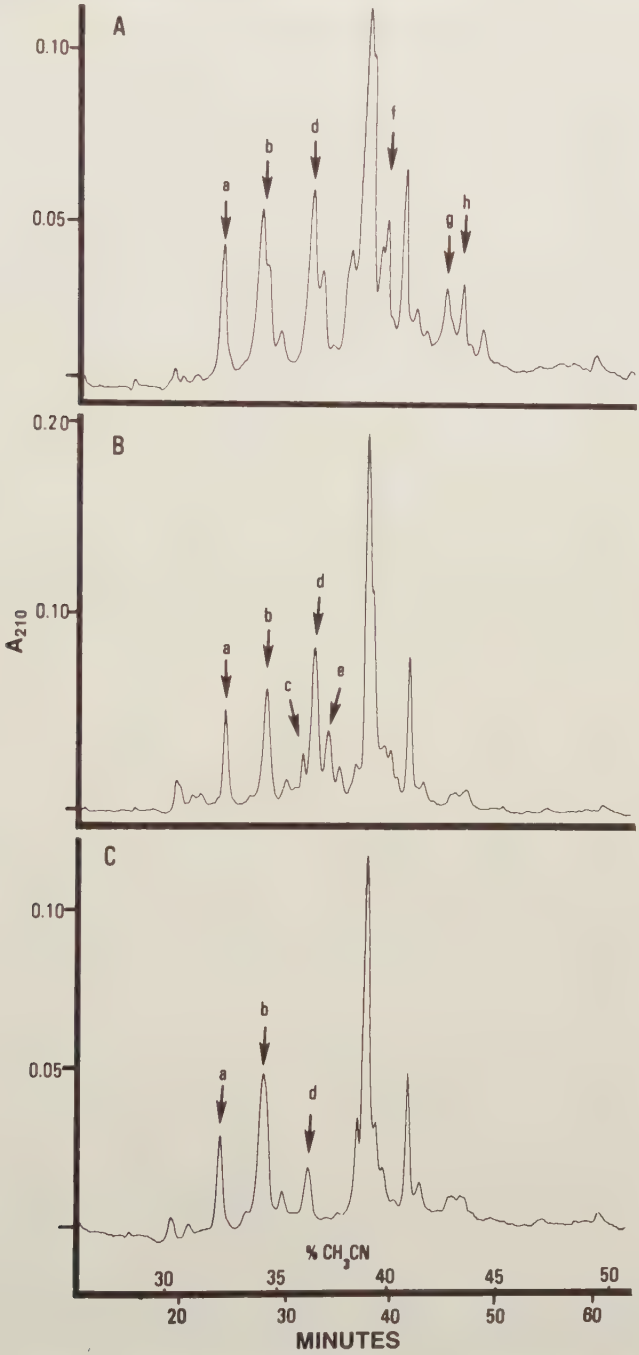

Fig. 5D–13. Variation related to breadmaking quality among high-molecular-weight glutenin subunits from the wheat cultivars (*A*) Marquis, (*B*) Hardi, and (*C*) Maris-Huntsman detected by reversed-phase high-performance liquid chromatography (RP-HPLC). From Burnouf and Bietz (1984b).

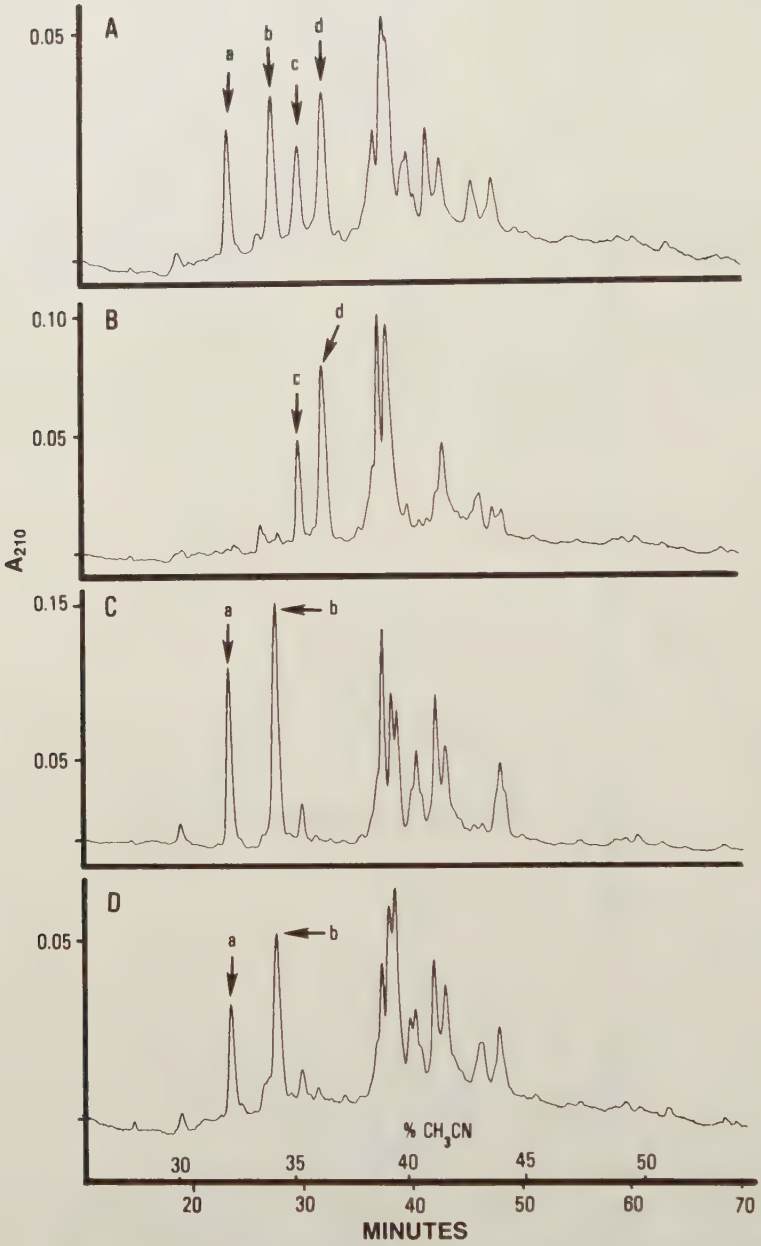

Fig. 5D–14. Reversed-phase high-performance liquid chromatography of pyridylethylated glutenin subunits from (*A*) the wheat cultivar Chinese Spring and from its aneuploid lines (*B*) nullisomic (N)1D-tetrasomic (T)1A (N1DT1A), (*C*) N1BT1A, and (*D*) Ditelo $1B_s$. From Burnouf and Bietz (1984b).

5D–2.2 Applications of Other HPLC Methods to Wheat Proteins

Although RP-HPLC has been the most successful HPLC technique applied to wheat proteins, size exclusion (SE) and ion exchange (IE) HPLC are also finding important applications. For example, resolution of wheat proteins by SE-HPLC (Bietz, 1984) is similar to that of traditional size-exclusion chromatography, but SE-HPLC has better reproducibility, accuracy, and ease of quantitation, and permits rapid (ca. 20 min) analyses in comparison to traditional methods, which may take days. SE-HPLC also may reveal differences in protein-MW distributions of wheat cultivars, which in turn may reveal bread-making quality.

Since ion-exchange chromatography is one of the best techniques for wheat protein fractionation, IE-HPLC should also be very useful (Bietz, 1985). Batey (1984) showed that resin-based "fast protein liquid chromatography" anion-exchange columns can identify wheat cultivars rapidly (in about 20 min) (Fig. 5D–15). Several other IE-HPLC columns tested, however, have not given good resolution of wheat endosperm proteins (J. Bietz, unpublished observations; I. Batey, CSIRO Wheat Research Unit, North Ryde, N.S.W., Australia, personal communication). It is probable, however, that a better understanding of how to use these columns, combined with improvements in columns themselves, will per-

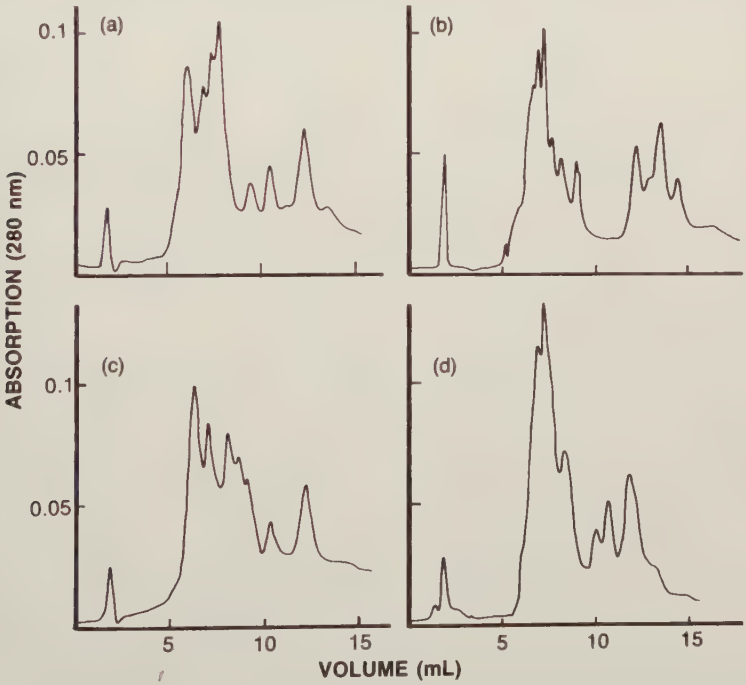

Fig. 5D–15. Separation of gliadin proteins by anion-exchange fast protein liquid chromatography (Mono-Q column, pH 10.4, gradient 0–0.5 *M* sodium acetate) for identification of the wheat cultivars (*a*) Condor, (*b*) Durati, (*c*) Egret, and (*d*) Eagle. From Batey (1984).

mit high-resolution IE-HPLC separations of wheat proteins, and will lead to further improvements in all other HPLC methods.

5D–3 IMMUNOCHEMICAL APPROACHES

Protein relationships based on electrophoresis or chromatography are necessarily indirect, because unique polypeptides could have similar size, charge distribution, and hydrophobicity; therefore, additional, more specific approaches are desirable. This section will briefly review one such approach, the use of immunochemical procedures, and will show their value in assessing structural similarity of proteins, and analyzing species and genome relationships. Reviews dealing with this subject include Ewart, 1977; Konarev et al., 1979; and Daussant and Skakoun, 1983.

Immunochemical reactions depend on the interaction of proteins (antigens) with antibodies, which are immunoglobulins produced by the defense mechanism of higher vertebrates. Each antigen may possess several structural features, known as antigenic determinants, for which unique antibodies are produced. Antigens and antibodies frequently interact to form insoluble complexes; this interaction may occur as they diffuse through a gel matrix, forming insoluble precipitin lines, as in double diffusion, immunoelectrophoresis, rocket immunoelectrophoresis, and crossed immunoelectrophoresis (Daussant and Skakoun, 1983). Newer methods offer additional advantages. ELISA techniques (enzyme-linked immunosorbent assays) rely on binding of enzyme-coupled reagents to antibodies, so that antigen-antibody complexes are ultimately detected by a sensitive coupled enzymatic reaction, making ELISA much more sensitive than other immunochemical procedures. ELISA has been successfully applied to gliadin (Windemann et al., 1982). Alternatively, proteins that have unusual solubilities and are not amenable to standard immunological assays may be analyzed after immobilization on a nitrocellulose membrane (Dierks-Ventling and Cozens, 1982) or chromatography paper (Esen et al., 1983).

Early immunological studies showed several gliadins to have common antigenic determinants, and suggested that gliadin and glutenin possess common structural features (Elton and Ewart, 1963; Grabar et al., 1965; Ewart, 1966; Beckwith and Heiner, 1966). These findings have been confirmed by sequence analysis (see below), but cross-contamination of gliadin and glutenin is possible in some studies.

Immunological comparisons of gliadins, albumins, and globulins have also been used to compare *Triticum* spp. and closely related genera. Proteins of the A, B, and D genomes of wheat have considerable structural resemblance (Ewart, 1966, 1969). However, some hexaploid wheat albumins characteristic of the D genome are absent in tetraploid wheat (Bozzini et al., 1970) and may reveal bread wheat in macaroni (Piazzi et al., 1972). Analysis of such proteins may best reveal genomic interrelationships among cereals (Konarev, 1981). Studies that examined antigenic

similarity of nongliadin proteins from *Triticum* spp. and closely related genera (Bozzini et al., 1970; Aniol, 1974; Konarev, 1981) confirmed knowledge of genome origins, and added some new knowledge concerning evolutionary relationships. However, in one study, using immunoelectrophoresis to assess phylogenetic relationships, enormous albumin/globulin variation was found within as well as between species (Rao, 1976). Limited cross-reaction has also been found between gluten proteins and similar prolamin fractions from fairly distantly related genera, such as *Hordeum* and *Zea* (Elton and Ewart, 1963; Kling, 1975; Dierks-Ventling and Cozens, 1982; Esen et al., 1983), indicating either significant sequence homology (as in ω-gliadin and C-hordein) or conservation of antigenic determinants representative of a common ancestor.

5D–4 PROTEIN SEQUENCE ANALYSIS

Determination of protein sequences is the ultimate technique for establishing genetic relationships. Electrophoresis and chromatography indicate only sequence similarity, since mutations may or may not lead to differences in charge, hydrophobicity, or size. This section briefly reviews the use of protein and nucleic acid sequence analysis to predict relationships and clarify origins of gliadin and glutenin polypeptides, and to determine evolutionary relationships among *Triticum* spp. and closely related genera.

Gliadin was first partially sequenced by Kasarda et al. (1974). Bietz et al. (1977) subsequently found two types of related gliadin sequences, as well as extensive homology within each group. One group consisted primarily of α- and β-gliadins, which are coded for by loci *Gli-A2*, *Gli-B2*, and *Gli-D2* on the short arms of chromosomes 6A, 6B, and 6D, respectively (Payne et al., 1984b). Another group, the γ-gliadins, had different though still homologous sequences coded by gene loci *Gli-A1*, *Gli-B1*, and *Gli-D1* on the short arms of chromosomes 1A, 1B, and 1D, respectively (Payne et al., 1984b). This homology suggests that gliadins originated through a process involving gene duplication, mutation, and polyploidy.

The complete sequences of three α-type gliadins have recently been determined from amino acid sequencing and from the sequences of cloned complementary DNA or genomic clones (Kasarda et al. 1984b, Anderson et al. 1984, Rafalski et al. 1984). Five sequence domains occur, two of which may have evolved from an ancestral gliadin gene. Significant homology occurs among these gliadins. In addition, Kasarda et al. (1984b) found evidence of homology between γ-3 and α-type gliadins.

Another group of gliadins, the ω-gliadins, have several variants of a significantly different sequence (Kasarda et al., 1983). These proteins, like γ-gliadins, are coded by the *Gli-A1*, *Gli-B1*, and *Gli-D1* loci (Payne et al. 1984b), and ω-gliadins are homologous to γ-3 gliadin (Shewry et al. 1980,

Kasarda et al. 1984a). Thus, in spite of considerable divergence, all gliadin proteins seem to share a common ancestor.

Homology among gliadins coded at various loci has permitted several intra- and intergeneric comparisons. For example, ω-gliadin from *T. monococcum* is homologous to barley C-hordein (Shewry et al. 1980), to ω-secalin of rye, and to ω-gliadins of tetraploid and hexaploid *Triticum* spp. (Kasarda et al. 1983). Similarly, rye secalins of 40 000 and 75 000 MW are homologous to *T. aestivum* γ-2 and -3 gliadins (Shewry et al. 1982). In addition, the marked homology among prolamins within most cereals permits sequence analysis of heterogeneous mixtures and use of the results to predict and clarify evolutionary relationships among genera (Bietz 1982).

Information is also becoming available concerning sequences of wheat glutenin subunits. Bietz and Wall (1980) first determined partial N-terminal sequences for low-MW ethanol-soluble subunits, which were identical to subunits of high-MW gliadin. Although their sequences differ significantly from those of other gliadins, they are synthesized by genes at the same complex loci on the short arms of chromosomes 1A, 1B, and 1D (*Gli-A1, Gli-B1*, and *Gli-D1*) that code ω- and γ-gliadins (Payne et al., 1984b).

Sequence information for high-MW glutenin subunits, coded by genes on the long arms of chromosomes 1A, 1B, and 1D (the *Glu-A1, Glu-B1*, and *Glu-D1* loci, respectively), is now also becoming available. Initial studies of these polypeptides revealed no free terminal amino groups (Bietz, Huebner, and Wall, unpublished observations); subsequently, this lack of reactivity was shown to result from acid-catalyzed cyclization of N-terminal glutaminyl residues to pyroglutamic acid, which is unreactive during Edman degradation (Shewry et al., 1984). In spite of these difficulties, Shewry et al. (1984) obtained partial sequence data for several high-MW glutenin subunits from *T. aestivum*, *T. monococcum*, and *Ae. squarrosa* (*T. tauschii*), which were shown to be homologous. DNA sequence analysis is now also rapidly revealing information about these subunits. Thompson et al. (1983) showed that high-MW glutenin subunits contain an internal 18-base pair repeat that codes the sequence -Gly-Gln-Gln-Pro-Gly-Gln-; similar results were obtained by Forde et al. (1984). These studies will soon reveal complete sequences for high-MW glutenin subunits, permitting better comparisons of proteins within and between genera, and finally offering the real possibility of relating protein structures to functionality.

5D–5 CONCLUSION

Several techniques, including electrophoresis, chromatography, immunochemistry, and sequence analysis of endosperm proteins, can be used to better understand the biology, biochemistry, and genetics of wheat. These proteins are extremely heterogeneous and their expression is nearly

constant, making them excellent genotypic indicators. Consequently, protein analysis can identify genotypes, trace or establish evolutionary relationships, and determine the chromosomal control, interrelationships, and origin of proteins. Such knowledge may be applied to taxonomy, and protein markers of specific characteristics may be identified. In addition, protein analyses allow screening for good quality, and improved knowledge of structures is leading to a better understanding of the contribution of proteins to dough functionality. Further improvements in these methods, as well as new techniques, will permit better separation, characterization, and comparison of wheat proteins to predict, measure, improve, and assure the good quality of wheat, our most important food crop.

5E Chromosome Banding Methods, Standard Chromosome Band Nomenclature, and Applications in Cytogenetic Analysis

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The 1970s and early 1980s have produced some of the most exciting developments in chromosome identification in plants and animals (Hsu, 1973). Among the many specialized Giemsa banding methods, two techniques, namely, C-banding and N-banding, have been most useful in cytogenetic studies of wheat and other cereals. Since the first reports on chromosome identification in common wheat by C-banding (Gill and Kimber, 1974a; Natarajan and Sarma, 1974; Zurabishvili et al., 1974) and by N-banding (Gerlach, 1977), there has been much progress and that work will be discussed herein. The main focus will be the comparison of and relationship between N-banding and C-banding techniques, the nomenclature and description of banded chromosomes of wheat, and the application of banding techniques in cytogenetic analysis of wheat and other cereal species.

5E–1 COMPARISON OF C-BANDING AND N-BANDING TECHNIQUES AND THE RELATIONSHIP BETWEEN C-BANDED AND N-BANDED HETEROCHROMATIN

The first reports on C-banding techniques dealt with animal chromosomes (Hsu, 1973), in which the bands were shown to consist of

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Wheat and Wheat Improvement—Agronomy Monograph no. 13. (2nd Edition).

constitutive (C) heterochromatin. Among cereal species, the first successful applications of C-banding techniques were demonstrated in rye (*Secale cereale* L.), triticale (X Triticosecale), and wheat (Merker, 1973; Sarma and Natarajan, 1973; Shchapova, 1974; Gill and Kimber, 1974a, 1974b, and 1974c; Verma and Rees, 1974; Vosa, 1974; Zurabishvili et al., 1974, 1978). The reports on rye clearly demonstrated that C-bands in somatic metaphase chromosomes were equivalent to constitutive heterochromatin found in pachytene chromosomes of rye (Gill and Kimber, 1974b, Shchapova, 1974).

Funaki et al. (1975) reported an improved N-banding technique that stained nucleolar-organizing regions (NORs) in animal and plant chromosomes. Gerlach (1977) and Jewell (1979) showed that whereas the N-banding technique might or might not specifically stain NORs in cereal species, it revealed specialized heterochromatin (N-bands) on nine of the 21 chromosomes of common wheat. Subsequently, Endo and Gill (1984a) identified 16 of the 21 chromosomes of common wheat by an improved N-banding technique.

The relationship between C-banded and N-banded heterochromatin has been obscure, however. Schlegel and Gill (1984) carried out sequential C- banding/N-banding analyses that revealed the C^+N^+ and C^+N^- heterochromatin in chromosomes of rye. Moreover, only C^+N^+ heterochromatin coincided with the localization of polypyrimidine DNA sequences (Dennis et al., 1980; Appels et al., 1982). Similarly, wheat heterochromatin can also be described as C^+N^+ and C^+N^- (Endo and Gill, 1984a). Again, only C^+N^+ heterochromatin exclusively coincided with the localization of polypyrimidine DNA sequences (Dennis et al., 1980; Appels et al., 1978). Therefore, C-banding and N-banding differentiation of heterochromatin has a biochemical basis; C-banding being a general technique for staining all classes of heterochromatin and N-banding revealing only specialized heterochromatin containing polypyrimidine DNA sequences. Thus, it follows that C-banding might be a widely applicable technique across plant and animal taxa and N-banding of limited use only to taxa containing significant amounts of polypyrimidine DNA sequences. Seal and Bennett (1982) also demonstrated heterogeneity of heterochromatin by combining the C-banding technique with different stains.

Although the C-banding technique allows identification of all chromosomes in wheat and other cereal species, and the N-banding technique identifies fewer chromosomes, N-banding does offer some advantages over C-banding. The N-banding procedure is rapid, extremely reproducible, often stains some bands more intensely, and also provides excellent resolution of bands (Endo and Gill, 1984a). Moreover, as discussed above, C-banding and N-banding techniques reveal a biochemical heterogeneity of heterochromatin (Jewell, 1981; Endo and Gill, 1984a; Schlegel and Gill, 1984). The following comparison is presented to bring out the salient features of C-banding (Gill and Kimber, 1974c; Bennett et al., 1977;

Iordansky et al., 1978; Seal and Bennett, 1981; Dvořák and Appels, 1982; Lukaszewski and Gustafson, 1983; Endo and Gill, 1984b) and N-banding procedures (Gerlach, 1977; Jewell, 1979; Endo and Gill, 1984a).

C-Banding	N-Banding
1. Treat root tips with ice water for 24 h; fix in 45% acetic acid overnight (but not longer than 20 h).	1. Treat root tips with ice water for 24 h; fix in a 3:1 ethanol (95%): acetic acid solution for 2–3 days at room temperature (longer storage is possible in the refrigerator at 0–4 °C).
2. Hydrolyze root tips in 0.2 *M* HCl for 50 to 60 min at room temperature; squash in 45% acetic acid; remove cover slip by freezing; treat in absolute alcohol for 1 h; air-dry and store in a desiccator overnight.	2. Soak root tips in 1% acetocarmine stain for 1 to 2 h; squash in 45% acetic acid; remove cover slip by freezing; treat in hot 45% acetic acid at 60°C for 10 min; air-dry overnight.
3. Treat slides in saturated barium hydroxide (5–10%) solution for 7 min; wash in distilled water; incubate in 2x SSC (0.30*M* NaCl-0.03 *M* Na citrate) solution at 52 to 60 °C for 1 h; rinse in distilled water.	3. Treat slides in hot 1 *M* NaH_2PO_4 at 94 °C for 2 min; rinse in distilled water.
4. Stain slides in freshly prepared Leishman or Giemsa solution.	4. Stain slides in freshly prepared Giemsa solution.

This comparison reveals important differences between the two techniques. C-banding requires $Ba(OH)_2$ treatment followed by incubation in 2x SSC buffer. In N-banding, the $Ba(OH)_2$ and 2x SSC treatments are replaced by a 1 *M* NaH_2PO_4 treatment at 94 °C. However, it is possible to modify the N-banding technique to obtain a C-banding-type pattern (Jewell, 1981). Conversely, N-banding-type patterns can be obtained by variations of the C-banding technique (Seal, 1982; Lukaszewski and Gustafson, 1983). The C-banded wheat chromosomes described by Seal (1982) are, in fact, N-banded, as they show banding patterns similar to N-banded wheat karyotype as described by Endo and Gill (1984a). As noted above, it is also possible to carry out sequential C-banding/N-banding on the same preparations to reveal the heterogeneity of heterochromatin (Schlegel and Gill, 1984).

5E–2 CHROMOSOME BAND NOMENCLATURE

In earlier studies on C-banding in wheat, Gill and Kimber (1974a) and then also Lukaszewski and Gustafson (1983) used standard genetic nomenclature to designate the chromosomes, but no attempt was made to develop a nomenclature for describing the bands. Iordansky et al. (1978) used the Generalized Cytological Nomenclature for Cereal Chromosomes (GCNCC) issued by the Paris Conference (1971) on standardization in human cytogenetics, to classify the chromosomes according to their length and describe the bands of the 21 chromosomes of common

wheat cultivars Diamont and Chinese Spring. Van Niekerk and Pienaar (1983) presented a comparison of previous C-banded idiograms with their own results and took initial steps in combining the genetic and GCNCC nomenclature. Their proposal is further amplified from more recent work and a standard banded karyotype of the common wheat cultivar Chinese Spring will be described here (Fig. 5E–1, –2, –3). It is anticipated that with widespread application of banding techniques in cytogenetic analysis, a need for a standard chromosome band nomenclature in wheat will be evident.

It should be noted that because of widespread banding polymorphism in many cultivars (Fig. 5E–2), the standard banded karyotype is based on Chinese Spring, which is a widely used cultivar for cytogenetic analysis in common wheat. Fortunately, there is no apparent banding polymorphism within Chinese Spring chromosomes except for a terminal band on 7A in some plants (Seal, 1982). The C-banded and N-banded chromosomes are shown in Fig. 5E–1; the idiogram of banded chromosomes in Chinese Spring depicted in Fig. 5E–3 is a composite diagram drawn from the C-banded and N-banded chromosomes shown in Fig. 5E–1. Information on chromosome size, centromere position, and arm ratio of individual chromosomes was obtained from the measurement of aceto-carmine stained and banded chromosomes (Table 5E–1). Furthermore, position, size, and intensity of individual bands are also important criteria in chromosome identification and are shown based on their relative size and position.

The designation of chromosome arms and bands follows the recommendations of the 1971 Paris Conference on standardization in human cytogenetics (Rowley, 1974). However, nomenclature in human chromosome banding was based on Q- and G-bands, whereas in wheat it is based on C- and N-bands. Under the proposed rules of nomenclature, each chromosome short arm is designated as p and the long arm as q. Each p and q arm is subdivided into regions based on chromosome landmarks. A chromosome landmark is defined as "a consistent and distinct morphologic feature that is an important diagnostic aid in identifying a chromosome." A region is defined as "any area of a chromosome lying between two adjacent landmarks." A band is defined as "a part of a chromosome clearly distinguishable from adjacent parts by virtue of its lighter or darker staining ability." Each arm consists of a continuous series of dark bands and light bands; by definition, there are no "interbands." Regions and bands are numbered consecutively from the centromere outwards along each chromosome arm (Paris Conference, 1971).

The two regions adjacent to the centromere are labeled *1* in each arm, the next, more distal regions, *2*, and so on. A band used as a landmark is considered as belonging entirely to the region distal to the landmark and is accorded the band number of *1* in that region. Each chromosome has a distinct centromere, and the heterochromatin bisected by the centromere is considered as two bands, each being labeled as *band*

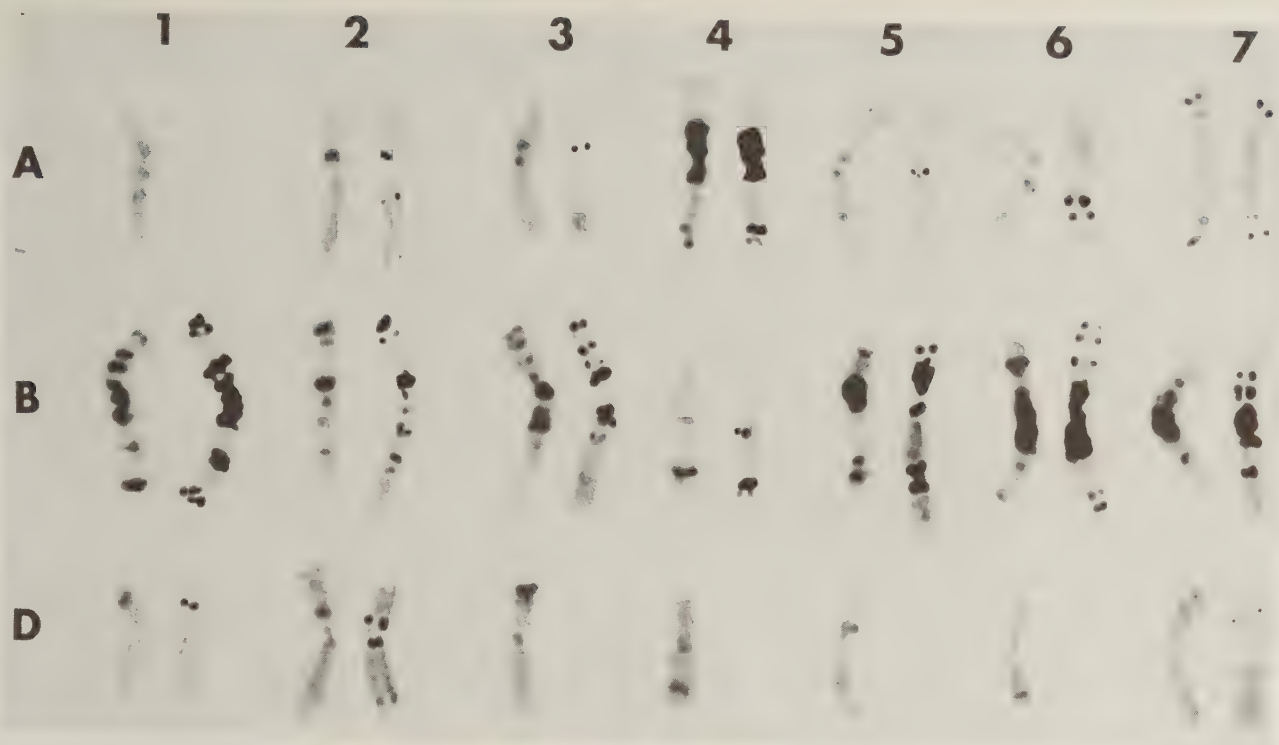

Fig. 5E–1. Comparison of 21 C-banded (*left*) and N-banded (*right*) individually paired chromosomes of *T. aestivum* cv. Chinese Spring. In each chromosome, the upper arm is the short (*p*) and the lower arm is the long (*q*) arm. (A diagrammatic representation of centromere position, arms, and bands is shown in Fig. 5E–3). Note that the C-banding technique reveals dark bands (constitutive heterochromatin) on all 21 chromosomes that can be individually identified. The N-banding technique reveals bands on only 16 chromosomes; chromosomes without N-bands are 1A, 3D, 4D, 5D, and 6D. Also note differences in C-banding and N-banding patterns in many chromosomes, including 4A, 5A, 6A, 7B, 1D, 2D, and 7D. These differences are caused by the heterogeneity of heterochromatin which has a biochemical basis (see discussion in text).

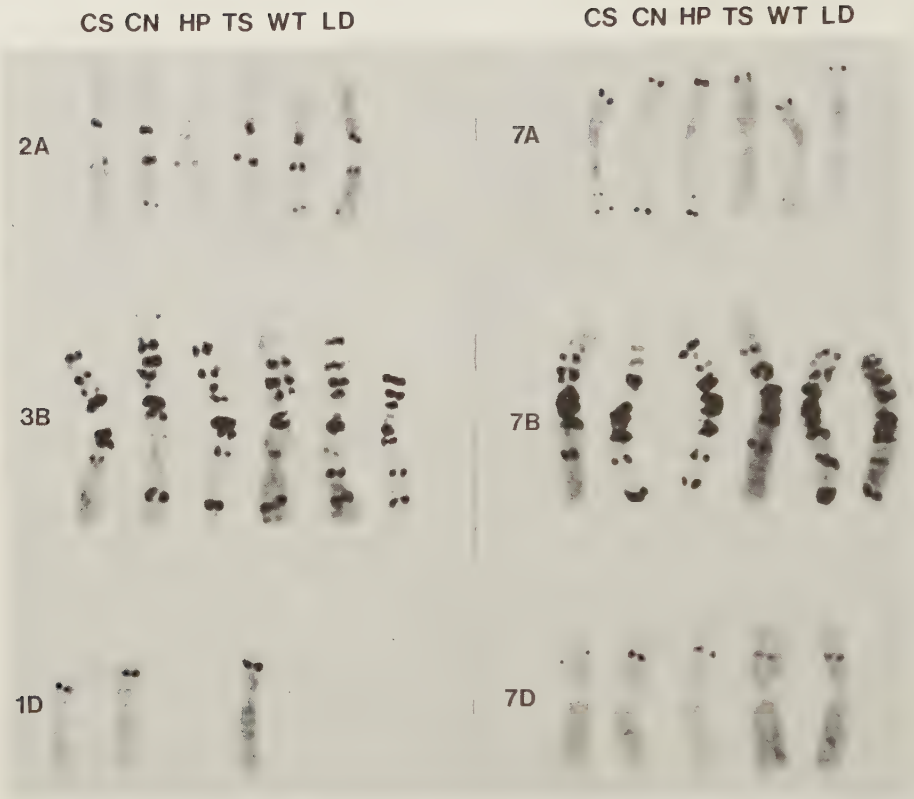

Fig. 5E–2 Examples of N-banding polymorphism for chromosomes 2A, 7A, 3B, 7B, 1D, and 7D of *T. aestivum* cv. Chinese Spring (*CS*), Cheyenne (*CN*), Hope (*HP*), Timstein (*TS*), Wichita (*WT*), and *T. durum* cv. Langdon (*LD*). In each chromosome, the upper arm is the short (p) and the lower arm is the long (q) arm. The polymorphism may involve presence vs. absence, or differences in the intensity, of bands. The banding polymorphism may be due either to the heterogeneity of heterochromatin or to structural changes.

1, in *region 1*, of the appropriate chromosome arm. Sometimes centromeric heterochromatin may extend into one arm and fuse with a proximal band, for example, the proximal band in the p arm of chromosome 2A (Fig. 5E–1 and 5E–2).

In designating a particular band, five items are required: the chromosome number, the genome designation, the arm symbol, the region number, and the band number within that region. These items are given in order without spacing or punctuation. For example, 1Bq21 indicates chromosome no. 1, genome B, long arm, region 2, and band 1.

Nomenclature rules on the subdivision of existing landmarks or bands state that "in the event that a band serving as a landmark requires subdivision, all sub-bands derived from it should retain the original region and band number of that landmark. This rule is to be followed even if subdivision should cause one or more sub-bands to lie in an adjacent

Table 5E–1. Somatic metaphase chromosome size and arm ratio of the 21 chromosomes of *T. aestivum* cv. Chinese Spring.

Arranged by size			Arranged by arm ratio (L/S) of homoeologues		
Chromosome	Size	(Arm ratio)	Chromosome	Arm ratio	(Size)
3B	13.8	(1.3)	5B	2.0	(12.1)
2B	12.9	(1.2)	5D	1.9	(10.4)
6B	12.7	(1.2)	5A	1.8	(11.5)
7B	12.5	(1.5)	1A	1.9	(11.1)
2A	12.5	(1.3)	1D	1.7	(8.4)
5B	12.1	(2.0)	1B	1.7	(11.8)
4B	11.9	(1.7)	4D	1.8	(9.0)
1B	11.8	(1.7)	4B	1.7	(11.9)
3A	11.5	(1.3)	4A	1.1	(11.4)
5A	11.5	(1.8)	3D	1.4	(10.7)
4A	11.4	(1.1)	3B	1.3	(13.8)
7A	11.3	(1.0)	3A	1.3	(11.5)
1A	11.1	(1.9)	2D	1.3	(10.1)
3D	10.7	(1.4)	2A	1.3	(12.5)
5D	10.4	(1.9)	2B	1.2	(12.9)
2D	10.1	(1.3)	6B	1.2	(12.7)
7D	10.1	(1.1)	6D	1.2	(9.9)
6D	9.9	(1.2)	6A	1.1	(9.8)
6A	9.8	(1.1)	7B	1.5	(12.5)
4D	9.0	(1.8)	7D	1.1	(10.1)
1D	8.4	(1.7)	7A	1.0	(11.3)

Measurements were made on acetocarmine-stained chromosomes that were identified by N-banding (data from Endo and Gill, 1984a), except for 1A, 3D, 4D, 5D, and 6D, where acetocarmine-stained chromosomes were identified by C-banding. The first three columns show that chromosomes of the B, A, and D genomes are of long, intermediate, and short lengths, respectively. In the next three columns, where homoeologous groups are arranged from high to low arm ratio, groups 5, 1, and 4 (excepting 4A) are highly heterobrachial and groups 6 and 7 (excepting 7B) are nearly metacentric. The exceptional arm ratio of 4A in Chinese Spring is due to an inversion; it is highly heterobrachial in other wheats. Chromosome 7B has an exceptional arm ratio in common wheat and tetraploid wheats (Endo and Gill, 1984a).

region. Whenever an existing band is to be subdivided, a decimal point should be placed after the original band designation followed by the number assigned to each sub-band. The sub-bands are numbered sequentially from the centromere outward. For example, if the original band 1q11 were subdivided into three equal or unequal sub-bands, the sub-bands would be labeled 1q11.1, 1q11.2, and 1q11.3, with sub-band 11.1 being proximal and 11.3 distal to the centromere. Finally, if a sub-band is to be subdivided, additional digits but no further punctuation should be used; e.g., sub-band 1p33.1 might be further subdivided into 1p33.11, 1p33.12, etc." (Paris Conference, 1971).

It can be seen that the proposed nomenclature provides the necessary accuracy and flexibility for describing banded chromosomes and any future additions to the bands. In common wheat, dark bands and light bands represent heterochromatic and euchromatic regions, respectively, and an attempt has been made to subdivide most wheat chromosomes into biologically meaningful regions. Thus, regions 1 and 2 in p and q

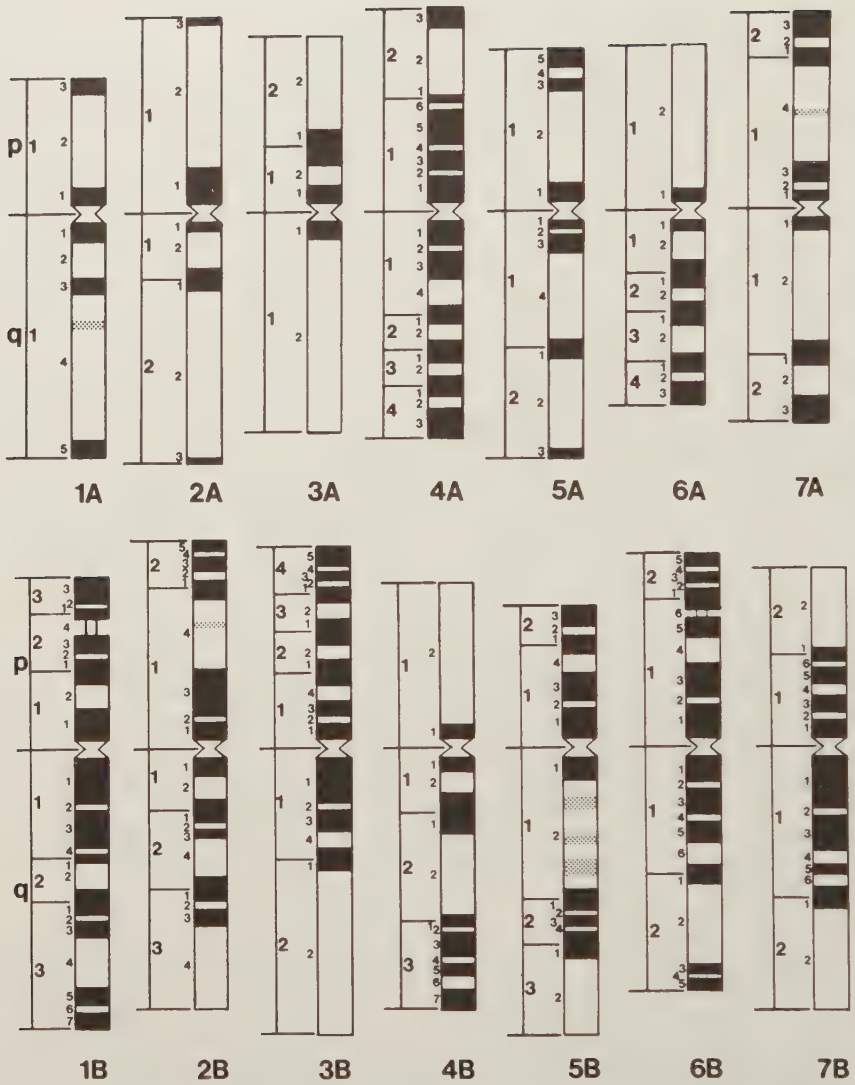

Fig. 5E–3. Idiogram and designation of bands in 21 chromosomes of *T. aestivum* cv. Chinese Spring according to the standard chromosome band nomenclature proposed herein (see discussion in text). *Continued on facing page.*

arms of 7B describe proximal heterochromatic and distal euchromatic bands, respectively.

Some nomenclatural modifications have been adapted to conform to special situations in wheat. Dark bands that are not always reproducible in all chromosomes are designated by stippled bands and have not been assigned band numbers. A good example is band 5Bq12. In some unusually clear preparations, this band can be subdivided and, if necessary, described as bands 5Bq12.1, 5Bq12.2, and so on.

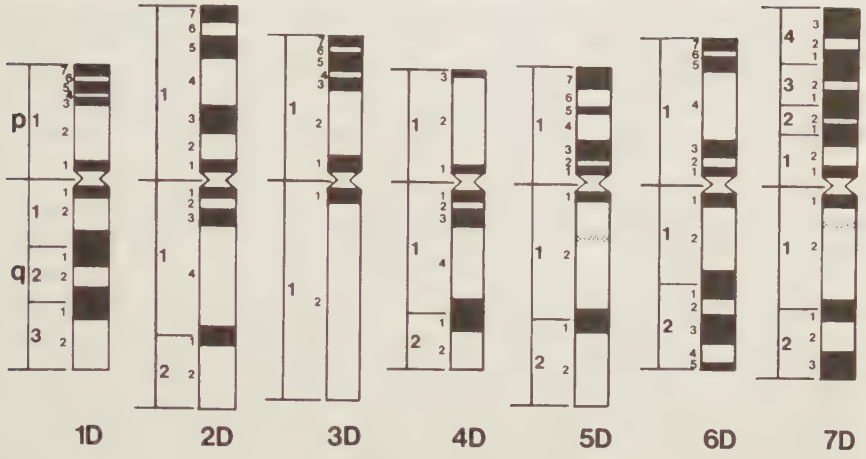

Fig. 5E–3. Continued.

In contravention to the intended meaning by the Paris Conference (1971), Hart (see section 5C, above), following Sears and Sears (1979), has used p and q to designate arm homoeologies within homoeologous groups. This poses problems for arm designation in chromosomes of homoeologous groups 2 and 4. Thus, arm 4Bq, which designates the long arm of chromosome 4B in our proposal, has been designated 4Bp by Hart, to indicate homoeology with 4Ap and 4Dp, short arms in both cases. One solution to this problem may be to amplify the designation in Hart's system to provide information on both homoeology and arm length. Thus, a designation p(L) would indicate that in the particular instance the p arm is actually the long arm. A designation of q(S) would indicate that in the particular instance the q arm is actually the short arm. Therefore, chromosome 4B, according to this system, will be designated as 4Bp(L) and 4Bq(S).

Space does not permit the detailed description of bands on all chromosomes, except as brief comments that may aid in the identification of certain chromosomes that could be confused with one another. Chromosome 1A can be distinguished from chromosomes 2A and 3A on the basis of arm ratios and the absence of any major landmark band. Chromosome 3A is distinguished from 2A by landmark band 3Ap21. The remaining A genome chromosomes are easily distinguishable.

In the B genome, 1B and 6B are the nucleolus-organizer chromosomes. Chromosome 3B has a large number of landmark bands in the p arm and can be distinguished from 2B on this basis. Chromosome 7B has proximal large, dark bands and distal large, light bands in each arm. The remaining chromosomes have many diagnostic landmarks and can be easily distinguished from one another.

In the D genome, chromosome 1D can be distinguished from 6D on the basis of arm ratio and bands 1Dq21 and 1Dq31. The banding pattern of chromosome 2D may often be confused with chromosome 5A and

can be distinguished on the basis of arm ratio and size. Moreover, band 2Dq21 is often fainter and tends to occupy a more distal position than 5Aq21 band. Chromosomes 3D, 4D, 5D, and 7D have highly diagnostic landmark bands and can be easily identified. The fact that chromosomes 1D, 4D, and 6D are among the smallest also helps in their identification.

5E–3 CHROMOSOME BANDING IN CYTOGENETIC ANALYSIS

The longitudinal differentiation of chromosomes revealed by the banding techniques provides a unique fingerprint of individual chromosomes and whole genomes for evolutionary studies. Several studies have been undertaken on the phylogeny of common wheat by banding analysis, but results were inconclusive (Gill and Kimber, 1974a; Natarajan and Sarma, 1974; Hadlaczky and Belea, 1975; Gerlach, 1977; Iordansky et al., 1978; Gill, 1981; Teoh and Hutchinson, 1983; Endo and Gill, 1984b). Some of the inconsistencies in banded karyotypes and evolutionary inferences drawn from such studies can be traced to intra- and interspecific banding polymorphism, and to the lack of standardization of banding techniques used in different laboratories.

Intraspecific banding polymorphism has been documented for different cultivars of wheat and rye (Giráldez et al., 1979; Endo and Gill, 1984a), different subspecies within a species (Teoh et al., 1983b) and between different species of a genus sharing a common genome (Singh and Röbbelen, 1975; Zurabishvili et al., 1978; Endo and Gill, 1984b). Intraplant banding polymorphism and the cytological mechanisms that may lead to it have been discussed in detail by Gustafson et al. (1983).

Conversely, chromosome pairing alone also may be inadequate in genome evolution studies. Banding and identification of individual chromosomes at meiosis has been reported in wheat and other species (Singh and Lelley, 1975; Jewell, 1979; Ferrer et al., 1984). Banding analysis of paired chromosomes at meiosis of intergeneric hybrids documented varying frequencies of autosyndetic, allosyndetic, and nonhomologous pairing that could not be detected in conventionally stained chromosome configurations (Thomas and Kaltsikes, 1974; Dhaliwal et al., 1977; Schlegel and Weryszko, 1979; Hutchinson et al., 1982, 1983).

Therefore, a combination of banding analysis of somatic and paired meiotic chromosomes in appropriate hybrids may provide precise determinations of phylogenetic and homoeologous relationships between chromosomes of wheat and related species (Chen and Gill, 1983; Gill et al., 1984). This method requires that chromosomes of alien species show some homologous or homoeologous pairing in hybrids with wheat. First, comparative observations are made on size, arm-ratio, and banding patterns of the karyotype of the alien species, and a possible homology with wheat chromosomes is predicted. Next, paired chromosomes in hybrids of double ditelosomics of wheat with the alien species are identified by

banding analysis, which indicates the genetic relationships of individually identifiable alien chromosomes (Fig. 4E–4). Using this technique, Chen and Gill (1983) showed that 4A-like chromosomes observed in *Triticum timopheevii* and *Aegilops* (*Triticum*) *speltoides* paired with 4A telosomes of durum wheat in *durum–timopheevii* and *durum–speltoides* hybrids. This supported studies on reallocation of the 4A chromosome to the B genome (Dvořák, 1983).

Banding techniques have also brought efficiency and a high degree of precision into studies on assays for the integrity of various cytogenetic stocks, the cytogenetic analysis of interspecific hybrids, and the isolation and identification of addition lines, substitution lines, and translocation lines. Gill and Kimber (1974a), and later Lukaszewski and Gustafson (1983), showed that a few telocentric stocks in Chinese Spring may have suffered deletions and otherwise may be misidentified. Singh and Röbbelen (1976) documented several cases of deletions within rye chromosomes in various wheat–rye addition lines. Similarly, monosomic stocks are known to undergo monosomic shift. This, along with the above observations, emphasizes that banding techniques should be used more often to verify the integrity of various aneuploid stocks in wheat.

Several reports document the usefulness of banding techniques in

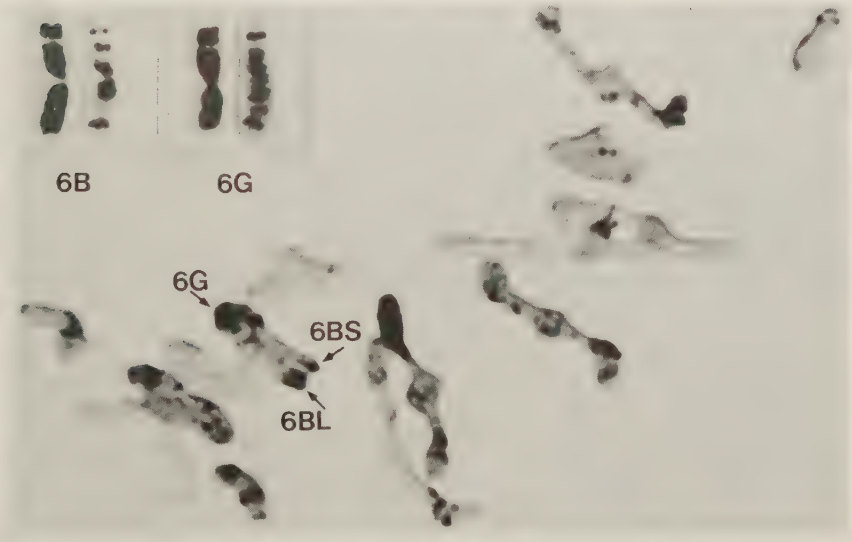

Fig. 5E–4 Demonstration of homoeology between chromosomes 6G of *T. timopheevii* and 6B of *T. turgidum* var. *durum* cv. Langdon by banding analysis of somatic metaphase and meiotic metaphase I (MI) chromosomes. The inset shows chromosome 6G (*right*); acetocarmine/N-banded) from *T. timopheevii* identified tentatively on the basis of comparative morphology with 6B (*left*) of *T. turgidum* var. *durum*. The main figure shows a N-banded MI cell of an F_1 hybrid between double ditelosomic 6B of *T. turgidum* var. *durum* with *T. timopheevii*, showing a trivalent 6BL.6G.6BS association and thus indicating homoeology between chromosomes 6G and 6B. Also note that most bivalents and trivalents involve banded (B—G) vs. unbanded (A—A) chromosomes.

isolating and identifying addition and translocation lines from intergeneric hybrids of wheat with other species (Islam, 1980; Jewell and Driscoll, 1983; Lukaszewski and Gustafson, 1983). Islam (1980) was able to identify by N-banding and designate the barley chromosomes added to wheat according to the standard barley (*Hordeum vulgare* L.) genetic nomenclature (Linde-Laursen, 1975; Noda and Kasha, 1978; Singh and Tsuchiya, 1982), a task which otherwise would have been accomplished only after many years of painstaking cytogenetic work. Jewell and Driscoll (1983) isolated nine addition lines of polyploid *Ae. variabilis* (*T. kotschyi*) (C^uS^v) in wheat and allocated these to genomes C^u or S^v from a comparative banding analysis with their putative diploid progenitor species chromosomes. Lukaszewski and Gustafson (1983) karyotyped 785 plants derived from triticale × wheat hybrids by C-banding and documented 195 wheat/rye and 64 rye/rye translocations, and 14 modified rye chromosomes. Moreover, they showed that most translocations involved complete arms and arose from misdivision and fusion of telocentrics derived from univalent chromosomes.

Another application of banding techniques that has been little explored is the physical mapping of genes in relation to cytological landmarks on chromosomes. A step towards this kind of cytogenetic mapping was taken by Dvořák et al. (1984) and Dvořák and Chen (1984), who tentatively mapped genes *Ph1b* and *Gli-B2* to specific bands on chromosomes 5B and 6B, respectively.

In spite of the innovation that banding techniques have brought to bear on cytogenetic analysis in wheat, this brief review must end on a note of caution. May and Appels (1980) were able to show that some triticales that previously were reported to contain modified 2R chromosomes had, in fact, translocated chromosomes involving 2B and 2R. Therefore, it is prudent to verify any apparent chromosomal aberrations by more conventional aneuploid and chromosome pairing analysis for the specific chromosome(s) implicated from banding analysis.

5F Aneuploid Analysis in Tetraploid Wheat

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Aneuploidy is an increase or decrease in chromosome number that does not involve an entire genome. The change in chromosome number may involve a single chromosome arm, as in the case of telosomics, or more than one chromosome, as in the case of the nullisomic-tetrasomics. A few of the more common aneuploids are defined in Table 5F–1 (after Kimber and Sears, 1970). Several different sets of aneuploids were produced in the hexaploid 'Chinese Spring' (CS) wheat (*Triticum aestivum* L.) by Sears (1954), including monosomics, nullisomics, trisomics, tetrasomics, and telosomics. These aneuploids have been used to locate genes on chromosomes, to map gene-to-centrometer distances, to transfer chro-

Table 5F–1. Types of wheat aneuploids and their descriptive terms and symbols.

Term	Meiotic configuration	
	Hexaploid	Tetraploid
Nullisomic	20″	13″
Monosomic	20″+1′	13″+1′
Disomic	21″	14″
Trisomic	20″+1‴	13″+1‴
Tetrasomic	20″+1^{IV}	13″+1^{IV}
Nullisomic-tetrasomic	19″+1^{IV}	12″+1^{IV}
Monotelosomic	20″+t′	13″+t′
Ditelosomic	20″+t″	13″+t″
Monotelodisomic	20″+1t″	13″+1t″
Double monotelosomic	20″+t′+t′	13″+t′+t′
Double ditelosomic	20″+t″+t″	13″+t″+t″
Dimonotelosomic	20″+t″+t′	13″+t″+t′
Monosomic addition	21″+1′	14″+1′
Disomic addition	21″+1″	14″+1″
Mono-wheat mono-alien substitution†	20″+1′+1′	13″+1′+1′
Di-alien substitution†	20″+1″	13″+1″

†Alien substitutions are designated by indicating the chromosome of the alien substitution followed by the wheat chromosome replaced; for example, 1R(1A) indicates that a pair of 1R chromosomes replaced a pair of 1A chromosomes.

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mosomes from one cultivar or species to another, and to identify chromosome homoeologies.

In contrast to hexaploid wheat, aneuploids in the tetraploids (*T. turgidum* L.) have been available only since the late 1970s. There are several reasons for this. First, the tetraploid wheats are grown on only about 10% of the land devoted to wheat production and, consequently, have received less attention in terms of research effort. Second, preliminary studies had indicated that aneuploidy is not as well tolerated in the tetraploids as in the hexaploids. Generally, reductions in chromosome numbers are more deleterious than increases in chromosome numbers. Consequently, nullisomic and monosomic plants of tetraploid wheat are not expected to be as vigorous and fertile as trisomics. The aneuploids available in durum wheat will be described and some suggestions for their use will be discussed.

5F–1 MONOSOMICS

Early attempts to produce monosomic lines of tetraploid durum wheat by crosses with hexaploid monosomics indicated that monosomic plants had low vigor, poor seed set, and low transmission of 13-chromosome (n-1) gametes. In hexaploid wheat, transmission of 20-chromosome (n-1) gametes averages about 75% through female and about 5 to 10% through male gametes. Mochizuki (1968, 1970) found that transmission through the female in backcrosses to 'Stewart' durum wheat averaged 2.6 to 30.2%. Hanchinal and Good (1982) found even lower transmission rates (mean = 1.68%) in backcrosses to 'Biyaga Yellow' durum. These low transmission rates, in conjunction with the low vigor and fertility of the monosomic plants, almost preclude the use of tetraploid monosomics for genetic analysis.

A few studies have tried to use hexaploid monosomics for genetic analysis of tetraploids. The method was to cross the hexaploid monosomics for the A- and B-genome chromosomes with tetraploid wheat. In the F_1 generation of each cross, plants were identified cytologically as either $2n=34$ (monopentaploid) or $2n=35$ (pentaploid). The F_1 monopentaploid plants were compared with the pentaploid plants; if they differed significantly, it was concluded that the missing A- or B-genome chromosome affected the trait. Allan and Vogel (1960), using CS monosomics and a smooth-awned durum wheat, located the genes for hooded, waxy bloom, and an awn inhibitor in CS, but failed to locate the gene for smooth awns. Kuspira and Millis (1967) used the 'Redman' monosomics to locate a gene for winter growth habit on chromosome 5A of the tetraploid 'Caid Elize.' Bozzini and Giorgi (1971) identified chromosomes affecting quantitative characters such as plant height, leaf length and width, maturity, and awn development. Each of these characters was affected by several chromosomes. Later, Bozzini and Carluccio (1973) crossed CS monosomic-5A (mono-5A) with eight durum lines and again

measured quantitative characters in the progeny. They concluded that monopentaploids could be used to locate factors affecting specific traits. However, they recognized that genes that were hemizygous (present in only one dose)-ineffective could not be recognized by these methods. Also, it was difficult or impossible to determine whether differences between the monopentaploid and the pentaploid were simply due to gene dosage or whether the two parents had different alleles for the trait under study.

One method for overcoming these difficulties is to substitute individual pairs of chromosomes from a tetraploid wheat into a hexaploid line by backcrossing repeatedly to the monosomic hexaploid parent (Fig. 5F–1). After several backcrosses, the genotype of the hexaploid parent should be recovered except for the pair of chromosomes substituted from the tetraploid. The method involves a lot of work and many cytological observations, but not as much work (because of fewer chromosomes) as substituting chromosome pairs from one hexaploid line into another. Disomic-substitution lines provide precise information regarding the effects of individual chromosomes on either qualitative or quantitative characters. Seed supplies need not be limiting, and replicated field experiments are feasible. In addition, Snape et al. (1975) and others have described elegant methods of determining quantitative inheritance and gene action using these disomic-substitution lines and their intercrosses.

In summary, monosomic tetraploids probably will not be used for genetic analysis because of the low transmission of n-1 gametes through both female and male gametes and the low vigor and fertility of the monosomic plants. Other types of aneuploids, which can be used for the same purposes as the monosomics, have been or are being developed.

Step 1: Cross all 14 monosomics of the A- and B-genomes of Chinese Spring by the tetraploid to be analyzed.

Generation	Select progeny with
F_1	$13'' + 8'$

Step 2: Backcross to respective hexaploid monosomic.

BC_1	$20'' + 1'$

Step 3: Check identity of monosomic chromosome by crossing with respective Chinese Spring double ditelosomic after 1st and last backcross.

Testcross	
Correct	$20'' + t' + t'$
Incorrect	$19'' + 1tt''' + 1'$

Step 4: Continue backcrossing to respective monosomic.

BC_2	$20'' + 1'$
.	.
.	.
BC_{6-8}	$20'' + 1'$

Step 5: Self, select disomics, and test for character under study.

Fig. 5F–1. Illustration of a method for producing disomic substitutions of chromosome pairs from tetraploid wheat into a hexaploid wheat.

5F–2 MONOSOMIC TRISOMICS

Longwell and Sears (1963) suggested that one method of overcoming the deficiencies of the tetraploid monosomics is to produce tetraploid wheat plants that are monosomic for one chromosome in the A- or B-genome and trisomic for the homoeologous chromosome in the other genome. They crossed the CS nullisomic-tetrasomics (nulli-tetras) with durum wheat and obtained progenies that were monosomic for chromosomes 2A, 2B, 3A, 5B, 6A, and 6B. In each case, the plant was trisomic for the homoeologous A- or B-genome chromosome. Noronha-Wagner and Mello-Sampayo (1966) continued developing the monosomic trisomics (mono-tris) of durum wheat but soon ran into problems of low fertility. In addition, it became apparent that some of the trisomics were tertiary trisomics; i.e., they had at least one translocated chromosome. In some cases, the translocation involved a D-genome chromosome (Mello-Sampayo, 1972).

Transmission of the mono-5B-tri-5A condition averaged 63% in selfed progenies. This rate is much higher than the transmission of monosomic durum chromosomes and would be high enough to be useful in genetic analysis. Mono-trisomics crossed with euploids can produce four types of plants. For example, mono-5B-tri-5A can give $12''+5B'+5A''$ ($2n=27$), $12''+5B'+5A'''$ ($2n=28$), $12''+5B''+5A''$ ($2n=28$), and $12''+5B''+5A'''$ ($2n=29$). The four types of F_1 plants can be distinguished by evaluating pairing at MI of meiosis. The monosomic F_1s of the critical cross should produce F_2 plants most of which have the phenotype of the euploid parent, as would be expected in a monosomic analysis of a hexaploid wheat. Furthermore, the F_2 progeny of the trisomic F_1 plants in the cross with the homoeologous mono-tri line should show trisomic inheritance; i.e., if the cross with mono-5A-tri-5B shows monosomic inheritance, then the F_2 progeny of the cross with mono-5B-tri-5A should show trisomic inheritance.

Unfortunately, a complete set of these aneuploids in durum wheat is unavailable. However, some related aneuploid sets such as primary trisomics (Simeone et al., 1983) and D-genome substitutions (Joppa and Williams, 1983) have been developed.

5F–3 TRISOMICS

Trisomics have been produced in a number of crop species such as barley (*Hordeum vulgare* L.), maize (*Zea mays* L.), rice (*Oryza sativa* L.), tobacco (*Nicotiana tabacum* L.), sorghum [*Sorghum bicolor* (L.) Moench], and tomato (*Lycopersicon esculentum* Mill.) and have been used widely for genetic analyses. Sears (1954) produced a set of tetrasomics (2n+2) in CS wheat from trisomics. Tetrasomics are even more useful than trisomics, because they transmit the tetrasomic condition to a large proportion of their selfed progeny. Trisomics transmit the trisomic condition

at variable rates depending on the chromosome involved. Gametes with n+1 chromosomes are seldom transmitted through the male and at variable rates (<50%) through the female.

Trisomics are classified as primary trisomics if all three chromosomes are homologous; secondary trisomics, if one of the chromosomes is an isosomic (having two arms the same); for example, 5Bq: 5Bq; and tertiary trisomics, if one of the chromosomes has a translocation. A complete set of primary trisomics in the durum cultivar Cappelli was developed by Simeone et al. (1983) by irradiation of pollen or by crossing the CS nullitetras with Cappelli followed by backcrossing to Cappelli. The identities of the trisomics were checked by crosses to the appropriate CS double-ditelosomics. These trisomics are vigorous and fertile and show different transmission rates (average = 27%) of the added chromosomes through the female gametes.

The durum wheat trisomics have not been used for genetic analyses as yet, but the methods should be similar to those used in other species. The identification of the chromosomal location of a gene using trisomics depends on the aberrant segregation ratios obtained in the cross with the critical trisomic. Since not all of the progeny of trisomic plants are trisomic, the first step is to germinate seeds of the trisomic lines and determine chromosome numbers in their root tips. Plants with $2n=29$ chromosomes are then crossed with the line or cultivar to be analyzed. The F_1 seeds are germinated, and chromosomes in root tips are counted. Plants with $2n=29$ chromosomes are selected and selfed and/or backcrossed to the line to be analyzed. For assumed transmission rates of 50 or 30% for $n+1$ chromosomes through the female gamete, and assuming there is complete chromosome segregation, the expected F_2 segregation in the critical cross is listed in Table 5F–2. Selfing the trisomic F_1 plants is more efficient than backcrossing, and simplex crosses (i.e., AAA by aa) are more efficient than duplex crosses (i.e., aaa by AA). The ratios listed are seldom obtained in practice, because the assumption of complete chromosome segregation is false unless the gene is completely linked to the centromere. Two possible explanations for deviations from expectation have been suggested. Random chromatid or maximum equational segregation of chromosomes during meiosis can produce occasional in-

Table 5F–2. Expected F_2 segregations of trisomic F_1s from the critical cross of trisomic by disomic, with no selection, no male transmission of $n+1$ gametes, and strict chromosome segregation.

F_1 genotype	Selfed or backcrossed to disomic recessive	Expected segregation if transmission of $n+1$ gametes through female is:	
		50%	30%
Aa	Self	3:1	3.0:1
Aa	BC	1:1	1.0:1
AAa	Self	17:1	11.9:1
AAa	BC	5:1	3.3:1
Aaa	Self	2:1	1.6:1
Aaa	BC	1:1	1.0:1.3

dividuals with the aaa genotype in simplex crosses and increase the proportion of recessives in the population. These trisomics should prove useful in determining the chromosomal location of genes in tetraploid wheat.

5F–4 D-GENOME DISOMIC SUBSTITUTIONS

Sears (1966b) divided the chromosomes of hexaploid wheat into seven homoeologous groups and showed that the chromosomes in different genomes, but in the same group, could compensate for each other in nullisomic–tetrasomic combinations. Thus, chromosome 1D compensates for 1A and 1B; chromosome 1B compensates for 1A and 1D; and chromosome 1A compensates for 1D and 1B.

Joppa and Williams (1983) recently produced a complete set of 14 different disomic-substitution lines with 13 pairs of durum chromosomes and a pair of D-genome chromosomes (Fig. 5F–2) by crossing the CS nulli-tetras (ie., nulli for an A- or B-genome chromosome and tetra for a homoeologous D-genome chromosome) with the durum wheat cv. Langdon (LDN). The F_1s with $13''+1''D+1'-A$ or $B+6'D$ were selfed and plants with $2n=28$ chromosomes were selected. In each case, a pair of D-genome chromosomes was substituted for the homoeologous A- or B-genome chromosomes. These lines contained genes from both CS and LDN. Since it was desirable to eliminate as many of the CS genes as possible, the lines were backcrossed to LDN at least five times. In each backcross generation, plants with the chromosome constitution $2n=13''+2'$ (i.e., monosomic for an A- or B-genome chromosome and for a homoeologous D-genome chromosome, Fig. 5F–2-D) were selected and backcrossed to LDN. After five backcrosses, the plants were selfed or crossed with a set of D-genome disomic-addition (Fig. 5F–2-A) lines followed by selfing, to produce the D-genome disomic-substitutions. Each of the lines was checked by crossing with the respective CS double-ditelosomics and with a set of LDN durum double-ditelosomics. Crossing a disomic-substitution line with the LDN double-ditelosomics will produce F_1 plants with $12''+1tt'''+2'$ if the chromosome substituted for is incorrect (Fig. 5F–2–E) and $13''+1'+t'+t'$ if the chromosome substituted for is correct (Fig. 5F–2-F).

Certain durum chromosomes, or chromosome arms, are essential at some point in the life cycle of the plant. Therefore, some disomic-substitution lines must contain a univalent or telosome of the critical A- or B-genome chromosome as well as a pair of compensating D-genome chromosomes (Table 5F–3). The essential chromosome arms are 3Bq, 5Aq, 5Bq, and 6Bp, with arm designations according to Sears and Sears (1979). The essential arm of chromosome 4B has not been determined. Transmission rates of the essential A- or B-genome chromosome are generally good (>25%), although the rate varies from plant to plant and from chromosome to chromosome. The 4B chromosome is particularly inter-

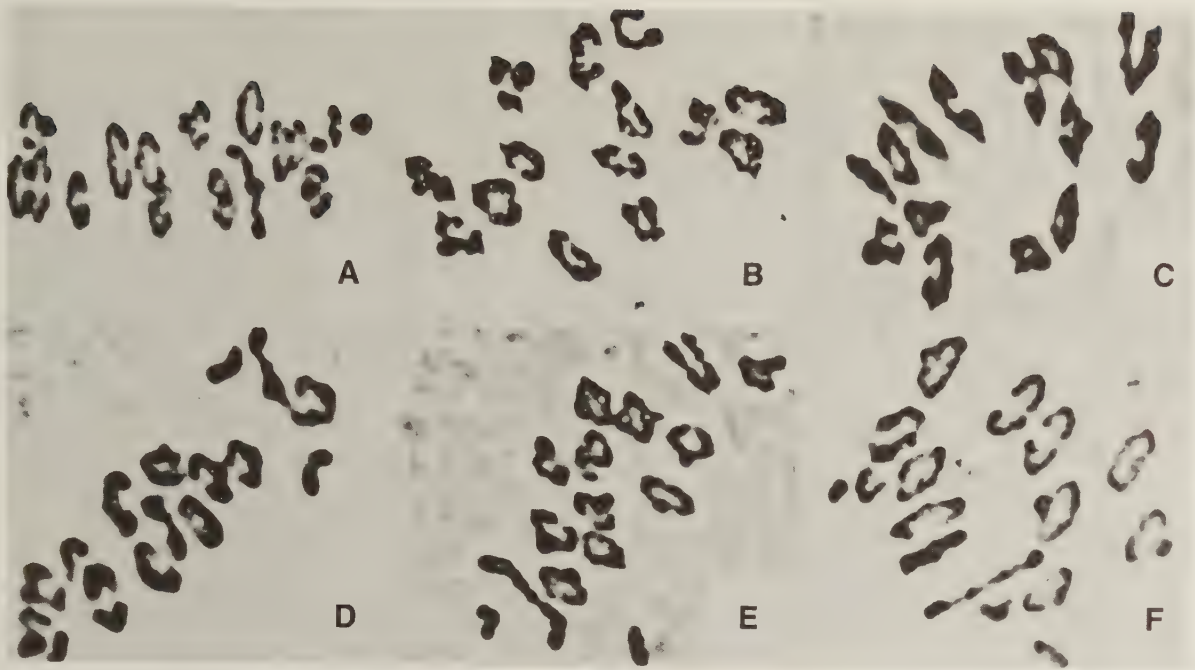

Fig. 5F–2. Chromosome pairing at metaphase I (MI) of meiosis in some aneuploids of tetraploid wheat: (*A*) 15 pairs in a 1D-disomic-addition line of Langdon durum; (*B*). a 1D(1A) disomic-substitution line of Langdon with 14 pairs of chromosomes; (*C*) a double telotrisomic plant with $13''+1tt'''$ from the cross CS double-ditelo 4B/4* LDN; (*D*) a 1D(1B) monosomic-substitution line with $13''+2'$; (*E*) $12''+1tt'''+2'$ in an F_1 plant from the cross of double-ditelo 3B by a 1D(1B) disomic-substitution line; (*F*) $13''+1'+t'+t'$ in an F_1 plant from the cross LDN double-ditelo 1A/disomic-substitution 1D(1A).

Table 5F–3. Comparisons among Langdon durum D-genome disomic-substitution lines for their relative vigor, fertility, and other characteristics.

Chromosome constitution				
D-chromosome substituted	A- or B-chromosome replaced	Vigor	Fertility	Other characteristics
1D	1A	Good	Good	Resembles Langdon
1D	1B	Good	Good	Short awns
2D	2A	Poor	Fair	Some female sterility
2D	2B	Fair	Good	Nonglaucous
3D	3A	Fair	Fair	Resembles Langdon
3D	3B†	Fair	Fair	Nulli 3B is desynaptic and sterile
4D	4A	Fair	Fair	Resembles Langdon
4D	4B‡	Poor	Poor	Semidwarf, compact heads
5D	5A†	Good	Poor	Nulli 5A is mostly male sterile, long rachis internode
5D	5B†	Good	Good	Homoeologous pairing
6D	6A	Fair	Fair	Short, early, good tillering, club head
6D	6B†	Fair	Poor	Nulli 6B is completely pistilloid, late-maturing, club head
7D	7A	Good	Good	Resembles Langdon, frequently awnless
7D	7B	Poor	Fair	Small seed, frequently awnless

†Maintained as 13″+D″+mono or telo for chromosome indicated.
‡All male gametes carry one arm of 4B. No nulli 4B plants obtained.

esting. The 4D(4B) line has been grown many times and used in a number of crosses. The data indicate that almost all functional male gametes have at least one arm of chromosome 4B, since no plants nullisomic for 4B have been found.

The disomic-substitution lines (Fig. 5F–3) can be used for (i) determining the chromosomal locations of genes; (ii) producing homologous, disomic substitutions of chromosomes from one line into another; and (iii) inducing translocations between homoeologous chromosomes in the case of the 5D(5B) line (Joppa and Williams, 1979).

The chromosomal locations of a number of gliadin polypeptides were determined by performing polyacrylamide gel electrophoresis (see section 5D-1.2.1, above) on the endosperm of single seeds of each of the disomic-substitution lines (Joppa et al., 1983b). The presence or absence of a particular chromosome was associated with the presence or absence of particular electrophoretic bands, and this association indicated the chromosomal location of the gliadin structural gene. Similarly, the chromosomal locations of Langdon durum genes for other proteins, enzymes, etc., can be determined using these lines.

The disomic-substitutions can be used in appropriate crosses to determine the chromosomal locations of genes in the A or B genomes by methods similar to those used in a monosomic analysis. Crosses between the disomic-substitution lines and durum wheat produce F_1 plants that are double monosomics, for a D-genome chromosome and the A- or B-genome chromosome for which it was substituted. For example, 1D(1A)/

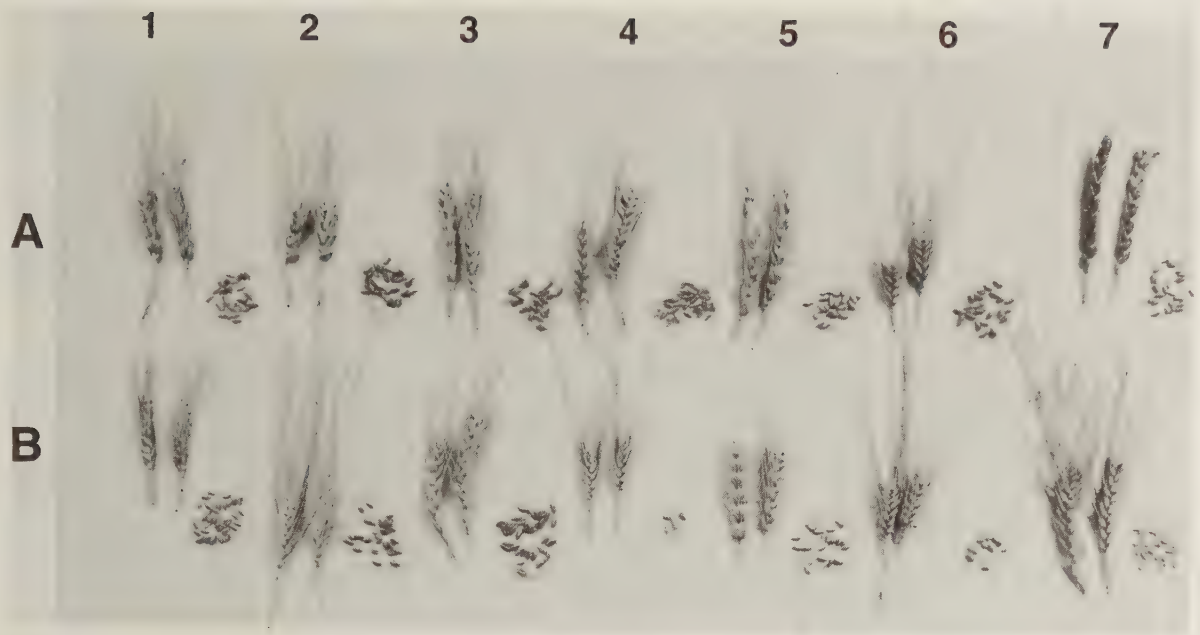

Fig. 5F–3 Spikes and seeds from each of the Langdon D-genome disomic-substitution lines. Seeds illustrate average number of seeds per spike.

'Golden Ball' gives an F_1 plant that has $13''+1_{1A}+1_{1D}$. The 1A chromosome must have come from Golden Ball and if it carries a recessive gene, then this F_1 will have the recessive phenotype—provided it is hemizygous-effective and provided that the homoeologous D-genome chromosome does not carry an epistatic gene for the same character. For example, genes for glume color have been reported on each of the group one chromosomes (*Bg* on 1A, *Rg1* on 1BS, and *Rg2* on 1DL; McIntosh, 1983). Langdon probably has *bg Rg1* and Chinese Spring has *rg2* on chromosome 1D. Crossing the 1D(1A) line with a black-glumed durum will produce black-glumed F_1 progeny only if *Bg* is epistatic to *rg2* on chromosome 1D. Epistatic relationships of homoeologous genes must be kept in mind when conducting any monosomic analysis, but may be particularly important when using the disomic substitutions.

The F_2 segregation is dependent on male and female transmission of the monosomic chromosomes. Possible F_1 gametes are $13'$, $13'+1'_{1D}$, $13+1'_{1A}$, and $13+1'_{1D}+1'_{1A}$. Female transmission of these gametes averages 9, 33, 39, and 16%, respectively (Joppa and Williams, 1977). Male transmission in F_1 plants is variable from one disomic-substitution line to another. Limited data indicates that chromosomes are transmitted through male gametes in approximate ratios of 13 = 0.4%, 13 + A or B = 73%, 13 + D = 19%, and 13 + A or B + D = 7.7% (Table 5F–4).

The frequency of various zygotes can be estimated by multiplying the transmission frequencies for various female gametes by the frequencies for various male gametes. Using the average female gamete fre-

Table 5F–4. Male transmission of monosomes in the F_1 generation from crosses between the D-genome disomic-substitution lines and various double-monosomic lines having $13''+1'_{A\text{ or }B}+1'_{D}$.

Double-monosomic	None	D-genome chromosome	A- or B-genome chromosome	Both A- or B- and D-genome	No. plants examined
1A+1D	0.01	0.20	0.75	0.03	93
2A+2D	0.00	0.26	0.65	0.10	31
3A+3D	0.00	0.13	0.85	0.02	53
4A+4D	0.00	0.49	0.46	0.06	70
5A+5D	0.00	0.07	0.75	0.18	85
6A+6D	0.00	0.28	0.63	0.08	60
7A+7D	0.00	0.26	0.71	0.03	108
1B+1D	0.00	0.37	0.60	0.02	86
2B+2D	0.03	0.19	0.68	0.10	104
3B+3D	0.00	0.13	0.81	0.06	79
4B+4D	0.00	0.04	0.75	0.21	84
5B+5D	0.00	0.10	0.87	0.03	91
6B+6D	0.00	0.00	0.89	0.11	57
7B+7D	0.00	0.12	0.82	0.06	49
Total plants:					
No.	4	199	766	81	1050
Freq.	0.004	0.190	0.730	0.077	

quencies from Joppa and Williams (1977) and the average male gamete frequencies from Table 5F–4, the expected zygote frequencies are: $13''=$ 0.04%, $13''+1'_{A\text{ or }B} = 6.7\%$, $13''+1'_{D} = 1.8\%$, $13''+1''_{A\text{ or }B} = 28.5\%$, $13''+1''_{D} = 6.3\%$, $13''+1'_{A\text{ or }B}+1'_{D} = 32.3\%$, $13''+1''_{A\text{ or }B}+1'_{D} = 14.7\%$, $13''+1'_{A\text{ or }B}+1''_{D}= 5.6\%$, and $13''+1''_{A\text{ or }B}+1''_{D} = 1.2\%$. If we assume a single dominant gene that segregates in the ratio 3:1 in noncritical crosses, then in the critical cross, only those F_2 plants nullisomic for the critical A- or B-genome chromosome ($13''$, $13'' + 1'_{D}$, and $13''+1''_{D} = 8.1\%$) will fail to express the mutant phenotype. Therefore, segregation in the F_2 should approximate a ratio of 11.5 plants with mutant phenotype to one nonmutant. An increase in the frequency with which the D-genome chromosome is transmitted, at the expense of the A- or B-genome chromosome, can reduce the frequency of progeny with the mutant phenotype. For example, the expected segregation ratio in the case of critical crosses with 4D(4A) is approximately 4.4:1 rather than 11.5:1. In those cases where the critical cross cannot be identified in the F_2, it may be necessary to testcross nonmutant F_2 plants with a normal tetraploid. The 28-chromosome testcross plants from the critical cross should all have $13''+2'$ at MI of meiosis, because the nonmutant plants must have been nullisomic for the critical A- or B-genome chromosome.

The 5D(5A), 3D(3B), 4D(4B), 5D(5B), and 6D(6B) lines are maintained as disomics for the D-genome chromosomes and monosomic or telosomic for the A- or B-genome chromosomes; therefore, these lines should be used as females in crosses. The F_1 plants from crosses with these lines must be investigated cytologically at MI of meiosis: plants having $14''$ or $14''+1'$ should be discarded, and plants with $13''+2'$ should be selected for further analysis.

The disomic-substitutions can also be used to substitute chromosomes from one cultivar or line into another. The general procedure is to cross the LDN disomic-substitution lines with a donor cultivar. The F_1 plants will be double monosomics (i.e., $13''+1'_{D} + 1'_{A\text{ or }B}$. Backcrossing these plants to the respective disomic-substitution lines will produce plants with $13''+1'$, $13''+2'$, $14''$, and $14''+1'$. The $13''+1'$, $14''$, and $14''+1'$ plants are monosomic or disomic for a D-genome chromosome and are discarded. The plants with $13''+2'$ are backcrossed to the respective disomic-substitution line in each succeeding generation for as many generations as necessary. After the last backcross, the plants with $13''+2'$ are selfed. Progeny with $14''$ are selected and testcrossed to durum or to the respective LDN double-ditelos. Those plants that have a pair of A- or B-genome chromosomes substituted into the LDN lines from the donor cultivar are grown for seed increase.

Joppa et al. (1983a) used the LDN 1D(1B) disomic-substitution line to substitute pairs of 1B chromosomes from 'Edmore' (EDM) and 'Kharkof-5' (KKF) into LDN durum. Langdon has weak gluten characteristics, whereas Edmore and Kharkof-5 have strong gluten. Langdon, Edmore, Kharkof-5, LDN 1D(1B), LDN-EDM 1B(LDN1B), and LDN-KKF 1B

(LDN1B) were compared in replicated field experiments at two locations. Sedimentation, mixograph score, spaghetti firmness, and loaf volume of the substitution lines were clearly superior to LDN and approached those of the nonrecurrent parents.

Producing substitution lines such as these requires considerable time and effort. However, no other method provides the researcher with better tools for assessing the genetic content of individual durum chromosomes.

5F–5 DOUBLE DITELOSOMICS

A complete set of double-ditelosomics for the A- and B-genome chromosomes has been developed in Langdon durum wheat by Joppa and Williams (unpublished) by crossing the CS double-ditelosomics to LDN and backcrossing plants with 13″+1tt′ ′ (Fig. 5F–2C) to LDN at least six times followed by selfing to obtain 13″+t″+t″. The LDN double-ditelosomics are fully fertile and vigorous, and resemble LDN in morphology. However, they may retain genes from CS, especially on telochromosomes. These lines have been used to identify chromosome substitutions. For example, the double ditelosomics were crossed with a durum wheat line having a pair of chromosomes substituted from *T. boeoticum*. The F_1s were grown, and chromosome pairing at metaphase I of meiosis was determined. All F_1s had 1tt‴+12″+2′ except for the cross with double ditelosomic 4B, which had 13″+1′+t′+t′. The data indicated that the *T. boeoticum* chromosome had been substituted for 4B. Little or no homology was observed between the *T. boeoticum* chromosome and any of the durum chromosomes (Joppa and Maan, 1982).

Sears (1966a) described a method for determining gene-to-centromere distances using ditelosomics. These same methods can be used with the double-ditelosomics by crossing to a euploid, backcrossing to the recessive, and classifying the backcrosses both cytologically and phenotypically to determine recombination percentage. However, the chromosome arm cannot be determined when double-ditelosomics are used instead of ditelos.

5F–6 OTHER TELOSOMICS

Some effort has been made to produce telosomics or ditelosomics of durum wheat. Nishikawa (1971) has a number of monotelodisomics (13″+1t″) or lines ditelosomic for one arm and telosomic for the other (13″+t″+t′, ditelomonotelodisomic) in Ld 222 durum wheat. Joppa (unpublished) also has a number of di-mono-telo lines in LDN durum. The latter set includes: 1Aq, 2Aq, 3Ap, 3Aq, 4Ap, 4Aq, 5Aq, 7Ap, 1Bq, 3Bq, 5Bq, 6Bp, 5Bq, and 7Bp. These lines have not been used in genetic or cytogenetic studies to date.

5F–7 SUMMARY

Complete sets of aneuploids in tetraploid wheat have only recently become available. The trisomic set in Cappelli, and the D-genome disomic-substitution set in LDN, were completed in 1983. These, together with the double-ditelosomics of Langdon and the partial sets of ditelomonotelos in Ld 222 and Langdon, make it possible to conduct most of the same types of genetic and cytogenetic analyses as in hexaploid wheat.

5G Gene Location and Gene Mapping in Hexaploid Wheat

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5G–1 GENE LOCATION

Despite the widespread availability of fully or partially developed series of monosomic lines in a wide range of hexaploid wheats (*Triticum aestivum* L.) from many countries (Table 5G–1), most gene-location work has been, and continues to be, based on the original 'Chinese Spring' series developed by Sears (1954) for the following reasons:

1. The Chinese Spring work is universally known and has been the basis for most wheat aneuploid work. Moreover, Chinese Spring probably remains the only complete naturally derived set of monosomics. Other complete sets have been produced by crossing the Chinese Spring set with particular cultivars and backcrossing selected F_1 monosomics with those cultivars.

2. In Chinese Spring there are several series of other aneuploid types, including monotelosomics and/or monoisosomics, double monotelosomics, ditelosomics, double ditelosomics, monoteloditelosomics, tetrasomics, nulli-tetrasomics, and double monosomics (combining monosomic 5B with all other monosomics). The majority of these, and others, have been produced and maintained by E.R. Sears.

3. Most Chinese Spring aneuploids can be assumed to be authentic, since they are available from Sears and from laboratories with much experience in aneuploid work.

4. Chinese Spring has a contrasting phenotype with respect to many individual characters of interest.

5. The breeding behaviors of Chinese Spring aneuploids have been

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Table 5G–1. Fully or partially synthesized monosomic lines of *Triticum aestivum* L., other than Chinese Spring, and country of origin.†

Country	Monosomic series
Australia	Condor Selection P44, Egret, Federation, Gabo, Gamenya, Gamut, Kenya W744, Oxley, Spica
Bulgaria	Bezostaya 1
Canada	Cadet, Kharkov, Lemhi, Prelude, Red Bobs, Redman, Rescue, S-615, Thatcher, Winalta
Egypt	Giza 144
France	Courtot
Germany (D.D.R.)	Alcedo, Carola, Poros, Qualitas
Germany (B.R.D.)	Caribo, Carsten VIII, Kranich, Jubilar, *T. spelta saharense,* Wachtel
Hungary	Mironovskaya 808, Rannyaya 12
India	Kalyansona, Pb C591
Italy	Mara
Japan	Nanbu-Komugi, Norin 10, Shinchunaga
Poland	Grana, Luna
Romania	Bezostaya 1, F307-65 (Favorit Selection)
Scandinavia	Starke
South Africa	Flameks, Inia 66, SST 3
Spain	Ariana 8, Aragon 03, Florence Aurore, Pane 247
Switzerland	Probus
USSR	Aurora, Bezostaya 2, Diamant II, Kaukaz, Kazakstanaskaya 12, Milturum 553, Novostepnayachka, Opal, Priboy, Saratovskaya 29, Skorospelka 35.
United Kingdom	Bersee, Cappelle-Desprez, Glennson, Hobbit Sib, Holdfast, Koga II.
USA	Cheyenne, Chris, Wichita
Yugoslavia	Sava, Novosadska, Rana 1

†Current status with respect to monosome authenticity, viability and degree of reconstitution of the recurrent parent is unknown to author.

established over a range of environments (Sears, 1954; Tsunewaki and Heyne, 1960).

6. Chinese Spring has what is regarded as the ancestral chromosome arrangement.

7. Chinese Spring has genes for high crossability with cereal rye and certain other related species.

Sears (1953) and Unrau (1950) outlined various procedures by which genes can be located in their respective chromosomes, while Sears (1962, 1966a) introduced the technique of telocentric mapping for the localization of genes to particular chromosome arms and for the estimation of gene-centromere recombination values.

The procedures of nullisomic/monosomic analysis depend upon the breeding behavior of the monosomics, upon the particular allele(s) present in the selected aneuploid series and whether the allele(s), especially when recessive, are expressed when present in the hemizygous (one-dose) state. The procedures are as follows.

5G–1.1 Nullisomic Method

In nullisomic analysis, observations are made for phenotypic differences between the nullisomic for each chromosome and the disomic (eu-

ploid) condition within the same cultivar. This method is suitable for the location of genes with positive function in wheat for which monosomics (or nullisomics) are available.

5G–1.2 Monosomic Method

When genes determining phenotypes of interest occur in wheat for which an aneuploid series is not available, crosses can be made to a monosomic series in a cultivar with the contrasting phenotype. The monosomics are used as female parents in order to ensure that the majority of progeny (ca. 72%) will be monosomic (Fig. 5G–1). If the gene involved is both recessive and hemizygous-effective, an unusual situation, direct phenotypic observations on F_1 monosomic progenies should enable location of the gene. Only monosomic individuals in the critical cross will exhibit the phenotype (fully or partially), whereas disomic sibs and monosomic (or disomic) progenies from all other crosses will display the dominant phenotype. If the selected monosomic series carries a dominant allele of the gene of interest, monosomic individuals in the critical cross usually exhibit the recessive phenotype, whereas disomic sibs display the dominant phenotype.

A dominant allele in the nonmonosomic parent may be located by examination of F_2 populations derived from selected monosomic F_1 plants. Recognition of the critical chromosome depends upon the breeding behavior of monosomics (Fig. 4G–1) and requires that the frequency of nullisomic plants with the nondominant phenotype permit easy distinction from the monogenic F_2 segregation ratios expected for the 20 noncritical crosses. In practice, this distinction is often demonstrated statistically, whereas cytogenetic confirmation tends to be infrequent. In order to confirm results, adult phenotypes and chromosome constitutions of at least a proportion of the individuals with nondominant phenotypes in the suspected critical population should be examined. A preponderance of plants is expected to be nullisomic, but other types also occur. These include: plants with telocentric or iso-chromosomes, which are monosomic or disomic, respectively, for the chromosome arm not carrying the gene; plants with $19''+1'''$ but nullisomic for the critical chromosome; and occasionally, in situations where enforced self-pollination has not

EGGS	POLLEN	
	21 chromosomes 96% (81–99)	20 chromosomes 4% (1–19)
21 chromosomes 25% (14–39)	Disomic 24% (11–39)	Monosomic 1% (0.1–7)
20 chromosomes 75% (61–86)	Monosomic 72% (49–85)	Nullisomic 3% (0.6–16)

Fig. 5G–1. Types and frequencies of progeny from self-pollination of a monosomic wheat plant. Average frequencies (and ranges, in parentheses) are based on experimental observations. From Morris and Sears (1967).

occurred, monosomic plants derived from outcrossing involving pollen with the recessive allele.

Another method that has been used for cytogenetic confirmation has been to determine somatic chromosome numbers of a further sample of F_2 plants from the suspected critical population and to correlate chromosome numbers with phenotypes. This is very useful in situations where nullisomic frequencies in the critical crosses are high.

While monosomic analyses using small F_2 populations are often clear-cut, various situations occur where results may be ambiguous. Some examples are as follows.

1. F_2 ratios may deviate from postulated Mendelian ratios. In such cases it may be possible to detect cytogenetic deviations by modified statistical tests. However, with 21 statistical tests, such as for a set of monosomic crosses, on average one result will show a significant chance deviation at $P=0.05$, hence the need for cytological confirmation of a gene location suggested by statistical analysis.

2. Unexpected genetic heterogeneities may be present, either within or between lines of the monosomic parent or within the euploid cultivar being analyzed. Within a cultivar, heterogeneities can be reduced by the use of single-plant selections in all genetic work. While genetic homogeneity can be achieved by such selection, results will be relevant to the parent-cultivar population only if the selection is representative of the majority of plants.

3. There may be higher than expected nullisomic frequencies, high rates of monosome misdivision, and outcrossing leading to F_2 segregation ratios not clearly distinguishable from the postulated euploid ratio.

4. Univalent shift (Person 1956) may occur in one or more of the monosomic lines, or in one or more of the gametes giving rise to the test monosomics. Univalent shift occurs when a 20-chromosome gamete receives the designated monosome but has spontaneously lost one of the other chromosomes. The possibility of monosomic lines becoming incorrect due to univalent shift can be reduced by experienced workers recognizing, in at least some instances, those meiotic monosomes not typical of the designated chromosome and by the frequent checking of monosomic plants used for seed production, against corresponding ditelosomics, or other distinctive cytological (see section 5E, above) or genetic markers. The risk of shift at the stage of crossing can be reduced by testing progenies from at least two different monosomic F_1 plants.

Anderson and Driscoll (1967) proposed the synthesis and use of monosomic alien substitution (MAS) lines in routine wheat monosomic work. The use of lines involving marked alien monosomes replacing the respective wheat homoeologues permits phenotypic selection of monosomic progeny lacking the alien chromosome and allows ready detection of univalent shift. Unfortunately this series remains incomplete (Bielig and Driscoll, 1973), and its use is restricted to the Chinese Spring background in which it was synthesized. However, the MAS condition could easily be transferred to other cultivars by backcrossing.

Another procedure aimed at detecting univalent shift is the routine use of monotelosomics or monoisosomics. Univalent shift is then detected in monosomic lines having paired telo- or isochromosomes: i.e., $19''+1t''+1'$, or $19''+1i''+1'$ (or $19''+2'+i'$). At present this is largely restricted to Chinese Spring. Monotelocentrics have a further advantage in that once a critical population is indicated, residue F_1 monotelodisomic sib plants, or their progenies, may be available for telocentric mapping. Unfortunately, monotelosomic plants for the homoeologous group 2 chromosomes are weak and/or late, but double monotelosomics ($20''+t'+t'$) can be used to generate monosomic F_1 plants.

5. As with other types of F_2 studies, the above experimental models assume accurate classification of F_2 phenotypes, but this is frequently not the case, especially where the genes being located determine disease resistance. Where classification of single F_2 individuals is difficult, tests of F_3 families allow the genotypes of F_2 plants to be established with certainty. Moreover, in instances where new genes are being studied, the accuracy of individual F_2 plant classification can be established only on the basis of progeny testing. Where a single gene is involved, F_2 progenies in noncritical crosses should be distributed as follows: 1 homozygous for the phenotype of interest; 2 segregating; 1 homozygous for the contrasting phenotype. The critical cross should have a reduced number of individuals in the latter homozygous group. Most importantly, in the critical cross those homozygous for the phenotype of interest should be disomic, with occasional monotelodisomics (critical-arm telocentrics); those segregating (with reduced numbers of contrasting phenotypes) should be monosomics, or occasionally monotelosomics (critical-arm telocentrics) or monotelodisomics (noncritical-arm telocentrics); and those homozygous for the contrasting phenotype should be nullisomic or monotelosomic (noncritical-arm telocentrics). If outcrossing of the F_1 has been permitted, occasional disomics may segregate (with normal F_2 ratios) and occasional monosomics will be nonsegregating for the contrasting phenotype.

Cytological analyses of F_2 plants can be performed in two ways. Meiotic analyses of individual F_2 plants involve the fixation and examination, or storage, of spikes in all crosses, since the gene location is not yet known. A more efficient procedure is to assess the F_3 lines and then to perform somatic chromosome counts on those populations considered most likely to involve the critical monosome. Somatic chromosome counts performed on F_3 progenies permit the deduction of the cytological status of the F_2 parent. A laboratory protocol commonly used at the University of Sydney is to set up for germination five kernels of each F_3, collect root tips from four seedlings, and stain root tips from three (keeping those of the fourth plant in reserve). Three seedlings with $2n=42$ is taken as evidence for disomy. As the probability of a disomic seedling from a monosomic parent is 0.24, the probability of three consecutive seedlings having $2n=42$ is $(0.24)^3=0.014$. On the other hand, any line with two

$2n=41$ seedlings is regarded as monosomic. Telocentric chromosomes, but not isochromosomes, are distinguishable at somatic metaphase; their usefulness when detected in critical populations was noted above.

If no potentially critical population is immediately obvious after phenotyping the F_3 progenies, chromosome determinations can be made on the F_3 lines homozygous for the phenotype of interest. Since in the critical cross such lines must be disomic, the detection of monosomic lines that are phenotypically homozygous can be used as a basis for rejection of a particular chromosome as a candidate for gene location. If no population becomes obvious after screening all monosomics, homozygous monosomic populations are then available for further cytogenetic manipulation, such as the pollination of monosomic F_3 individuals with corresponding ditelocentric lines. A search can then be made for univalent shift that could account for earlier failures, and with these materials the entire cytogenetic study can be repeated. In this case the progenies of the monotelosomic testcross individuals in the critical line should be homozygous for the contrasting phenotype and only the monotelodisomic sibs should segregate. Monotelosomic progenies in all noncritical crosses should segregate.

Locations of single recessive genes are difficult because in the critical cross, the 24% disomic and homozygous individuals cannot be statistically distinguished from the 25% homozygotes deriving from normal segregation. Where F_2 phenotypes are clearly expressed, somatic chromosome counts and phenotype analyses can be performed on F_2 populations; alternatively, F_3 studies can be performed as outlined above.

For planning purposes, note that a skilled technician typically can perform 80 to 100 somatic chromosome determinations each day.

5G–1.3 Substitution Method

The substitution method is more appropriate for the location of genes determining characters with a complex genetic basis. By backcrossing, each chromosome of a donor wheat is introduced separately into a recipient cultivar where a series of monosomic lines is available. This is achieved by manipulating the chromosome of the donor as a monosome that cannot undergo recombination, while the genetic background of the recurrent parent is reconstituted in accordance with the rules of backcrossing. About six backcrosses are carried out before the final monosomic is selfed, prior to selection of the disomic substitution line.

Because substitution lines are reconstituted by backcrossing, a small proportion of genes from the donor will remain and, since each of the 21 substitutions is produced independently, the remaining chromatin will vary randomly among the lines. A sixth backcross monosomic plant will continue to be heterozygous for $(\frac{1}{2})^6 = 0.0156$ of the genes by which it differed from the donor parent. Upon selfing, 25% of the donor genes will be lost by chance, hence a first-generation substitution line has a probability of about 1% of being either homozygous or heterozygous for

a donor parental gene that is not present in the substituted chromosome. However, in a set of 21 lines the probability of a nominated gene being present in one noncritical line increases to about 20%. McIntosh et al. (1967) identified two substitution lines, 6B and 7B, of the Chinese Spring ('Hope') series produced by Sears et al. (1957) that possessed *Sr17*. That *Sr17* was located in chromosome 7B, rather than 6B, was resolved with the use of a monosomic series in 'Redman' that also carried *Sr17*. The relatively high probabilities of particular genes being present by chance in chromosome substitution sets makes it essential that chromosome location based on the method be confirmed by further manipulations.

The synthesis of chromosome substitution lines is not without other problems. As a method of cytogenetic analysis of genetically complex characters, it is assumed that the disomic genetic backgrounds of the 21 monosomic lines used as recurrent parents are genetically (and phenotypically) identical. From the nature of their development this seems unlikely even in the original Chinese Spring series, and since most other monosomics have been developed as independent backcross derivatives, some variation will remain. Random mutational changes within monosomic lines will add to such differences.

The synthesis of a set of chromosome substitution lines requires a large number of technical manipulations, including sampling for chromosome number determinations, crossing, and the manipulation of seeds and plants, all dependent on the absence of human error. In addition, various types of biological error are difficult to detect, and recommended procedures to minimize their occurrence may be labor- and time-consuming. For example, one important change in the synthesis of a substitution series where a monosomic series is used as the recurrent female parent and the resultant monosomic F_1 is recycled as male parent, is the instance where a 21-chromosome egg combines with a 20-chromosome pollen grain (1%; see Fig. 5G–1); the resultant F_1 has the target chromosome of the recurrent, rather than donor, parent. In order to obviate this problem, monotelosomic, monoisosomic, or double monotelosomic recurrent parents can be used. However, even in Chinese Spring the possible genotypic and phenotypic differences between recurrent parents of the series is impossible, or extremely difficult, to determine, since disomics cannot be extracted for direct comparisons. No similar series is available in other genetic backgrounds. An alternative procedure is to extract disomic progeny from monosomics following each backcross to the recurrent parent for use as male parents in the next backcross. This doubles the time, and increases the number of technical manipulations involved in producing a substitution series. As a compromise, Law and Worland (1973) suggested the synthesis of independent duplicate sets of lines. Deviations involving duplicate lines would indicate those instances where genes affecting a character are located in substituted chromosomes.

During the synthesis of a substitution series, univalent shift in a female gamete of a correctly designated monosomic line can usually be

recognized only at meiotic metaphase (and only in some instances) before the plant is used in further backcrossing. In the case of the CS(Hope) series (Sears et al., 1957), *Sr9d* (*Sr1*) was not present in the CS('Hope' 2B) line which, on the basis of subsequent data (Loegering and Sears, 1970) should have carried it. Singh and McIntosh (1984) found that a CS('Ciano' 3B) line failed to carry *Sr2* which was known to be located in chromosome 3B. On the other hand, *Sr2* was present in a CS(Ciano 5B) line, presumably due to chance transfer during backcrossing.

5G–2 GENE MAPPING

The possibility of gene mapping in wheat usually arises when one or more genes have been located to a particular chromosome. Two types of gene mapping are commonly employed: first, in instances of populations segregating jointly for two or more genes, and second, in telocentric mapping, where a telocentric chromosome can be used as a cytological marker in place of a second genetic locus, hence enabling a single gene locus to be mapped in relation to the centromere. Conventional two-locus linkage analysis will be considered first, as telocentric mapping may be regarded as a special case.

5G–2.1 Conventional Gene Mapping

The normal procedure in the analysis of joint segregation data irrespective of whether the genes responsible are known to be located in the same chromosome, is to test for genetic independence by means of a chi-square analysis. If the genes do not segregate independently, estimates of genetic linkage can be made. Methods of estimation vary with the type of data. As wheat is normally self-pollinating, the development of large testcross populations by controlled crossing can be time-consuming. On the other hand, data from self-pollinations are more difficult to analyse, although routine methods of analysis are available for most situations. Moreover, the relative efficiencies of testcross and selfing vary with dominance, linkage phase of the dominant alleles (i.e., coupling [*AABB/aabb*] or repulsion [*AAbb/aaBB*]), degree of genetic linkage, and the method by which progenies are analyzed. The frequent need to progeny-test single individuals, i.e., progenies of testcross F_1, or of F_2, in instances where phenotypic classifications are not clear-cut, was discussed above. Analyses based on genotypes (where genes are incompletely dominant, or where progeny tests have been performed), rather than phenotypes, are always the most efficient (Allard, 1956; Westcott et al., 1978). Additionally, the confirmation of rare recombinant genotypes in instances of very close genetic linkage, and their storage in germplasm collections for future reference should be encouraged. Assuming a heterozygote with two linked genes *A/a* and *B/b* and recombination value p, the gametic frequencies are as follows:

	Expected frequency with linkage in		Observed frequency
	Coupling	Repulsion	
AB	½(1−p)	½p	a
Ab	½p	½(1−p)	b
aB	½p	½(1−p)	c
ab	½(1−p)	½p	d
		Total	N

On testcrossing (to *aabb* individuals), the expected distribution of progeny phenotypes reflects the gametic frequencies, and p can be estimated as the proportion of progeny with nonparental genotypes, assuming that the phenotypes for each gene are distinctive, i.e.,

$$p = b+c/N \quad [1]$$

and the variance of p can be estimated as

$$s_p^2 = [p(1-p)]/N \quad [2]$$

Table 5G–2 lists the phenotypic and genotypic distributions following

Table 5G–2. Observed and expected frequencies of F_2 phenotypes and genotypes occurring in the selfed progeny of an *AaBb* individual when the loci are genetically independent (column 2) and when linked (columns 3, 4, and 5) with a recombination value of p. From Allard (1956).

	Genetic independence		Expected frequencies Linkage in: Coupling	Repulsion	Observed frequency
Phenotype					
A-B-	9		¼(3−2p+p²)	¼(2+p²)	a
A-bb	3		¼(2p−p²)	¼(1−p²)	b
aaB-	3		¼(2p−p²)	¼(1−p²)	c
aabb	1		¼(1−p)²	¼p²	d
					N
Genotype					
AB/AB	1		¼(1−p)²	¼p²	e
AB/aB	2	9	½p(1−p)	½p(1−p)	f
AB/Ab	2		½p(1−p)	½p(1−p)	g
AB/ab†	4		½(1−p)²	½p²	h
Ab/aB†			½p²	½(1−p)²	i
Ab/Ab	1	3	¼p²	¼(1−p)²	j
Ab/ab	2		½p(1−p)	½p(1−p)	k
aB/aB	1	3	¼p²	¼(1−p)²	l
aB/ab	2		½p(1−p)	½p(1−p)	m
ab/ab	1	1	¼(1−p)²	¼p²	n
					N

†Usually not distinguishable.

self-pollination of the same heterozygote, assuming random transmission of male and female gametes. While variations in phenotypic distributions will occur with different types of gene interaction, expectations for the most common and general cases are listed in the table.

Linkage estimations are based on the method of maximum likelihood; various formulae for the estimation of p in a range of genetic situations are given by Allard (1956). In addition, he provides formulae for the calculation of the mean amount of information (i_p) per F_2 individual, or F_3 line, needed in estimating a standard error for p. The total information (I_p) provided by a particular family is Ni_p.

As

$$s_p^2 = 1/I_p \qquad [3]$$

$$s_p = (1/I_p)^{1/2} = (1/Ni_p)^{1/2} \qquad [4]$$

The maximum likelihood equation for estimating p from a repulsion-phase cross with full phenotypic classification (Table 5G–2) is

$$a\left(\frac{2p}{2+p^2}\right) + (b+c)\left(\frac{-2p}{1-p^2}\right) + d\left(\frac{2}{p}\right) = 0 \qquad [5]$$

i.e.:

$$\frac{a}{2+p^2} - \frac{(b+c)}{1-p^2} + \frac{d}{p^2} = 0 \qquad [6]$$

and

$$i_p = \frac{2(1+2p^2)}{(2+p^2)(1-p^2)} \qquad [7]$$

With complete genotypic classification except for distinction of the two double heterozygotes, namely *Ab/aB* (parental) and *AB/ab* (recombinant), the maximum likelihood equation is:

$$(e+n)\left(\frac{2}{p}\right) + (f+g+k+m)\left(\frac{1-2p}{p(1-p)}\right) +$$

$$(j+l)\left(\frac{2}{p-1}\right) + h+i\left(\frac{2(2p-1)}{(1-2p+p^2)}\right) = 0 \qquad [8]$$

and

$$i_p = \frac{2(1-3p+3p^2)}{p(1-p)(1-2p+2p^2)} \quad [9]$$

The and McIntosh (1975) investigated an instance where genetic ratios attributable to segregation at a single locus (e.g., *Sr22/sr22*) differed from that expected from random gametic transmissions. A corrected male transmission rate was estimated and applied in linkage estimation. However, the correction had only small effects on the separate linkage estimates of approximately 2 and 40% involving three genes.

5G–2.2 Use of Telocentric Chromosomes In Gene Localization

The absence of a particular phenotype in mono- or ditelocentric (and corresponding isochromosome) lines implies that the gene(s) determining the phenotype are located in the missing chromosome arm. For example, Chinese Spring plants mono- or ditelosomic for chromosome 6BS are awned, implying the presence of the awn inhibitor *B2* in the long arm, 6BL. On the other hand, Chinese Spring plants mono- or ditelosomic for 3DL have red pericarp. Since *R1* determining pericarp color in this cultivar is known to be located in chromosome 3D, *R1* must occur in 3DL, a deduction that was confirmed following the isolation of a ditelosomic 3DS line. One advantage of direct observations on mono- or ditelosomic lines (as well as nullisomics and nulli-tetrasomics) is that allelic variation is not essential for chromosome location of genes controlling characters of positive effect. This has been important in the chromosome location and arm localization of many isozyme-producing genes in wheat. However, allelic variation is essential for gene mapping, except for the relatively few instances where this has been achieved by deletion mapping or as a consequence of alien genetic exchange (Hart et al., 1976).

Evidence for arm location of a gene may arise as a consequence of monosomic analysis. As already indicated, in addition to nullisomics, individuals monotelosomic or monoisosomic for the noncritical chromosome arm may occur among those few F_2 individuals with the contrasting phenotype in the critical monosomic population. Such telosomes or isosomes can be checked against the standard telocentric chromosomes in Chinese Spring to confirm the identity of the misdivided chromosome product and the particular arm involved. By inference, the gene of interest must be located in the opposite arm. In some situations cytological examinations of individuals with the dominant phenotype may detect telocentric chromosomes. If monotelosomic, they can be checked against the standard telosome and can be progeny-tested to confirm that the gene is actually present in the telosome. Some individuals in the dominant phenotypic class may be monotelodisomic (Figure 5G–2). The use of these as female parents in crosses with a standard telosomic source of the candidate chromosome, and cytological examination of those progeny with two telosomes enables confirmation of the identity of the telosome

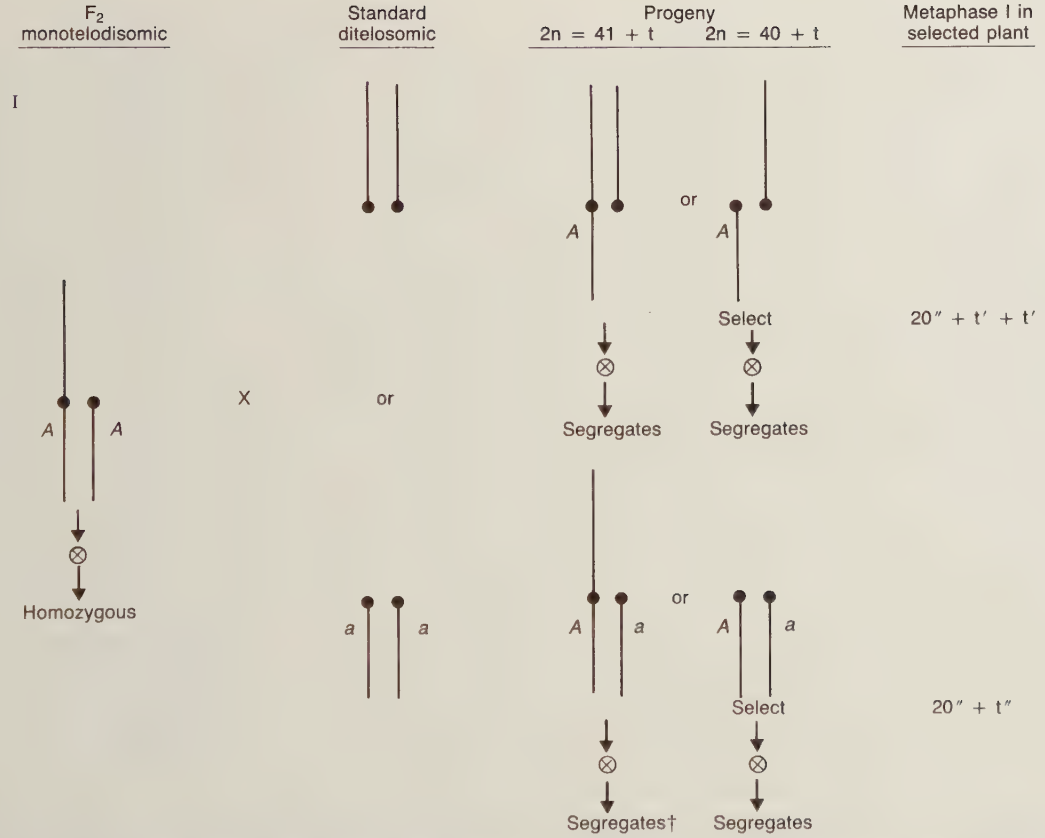
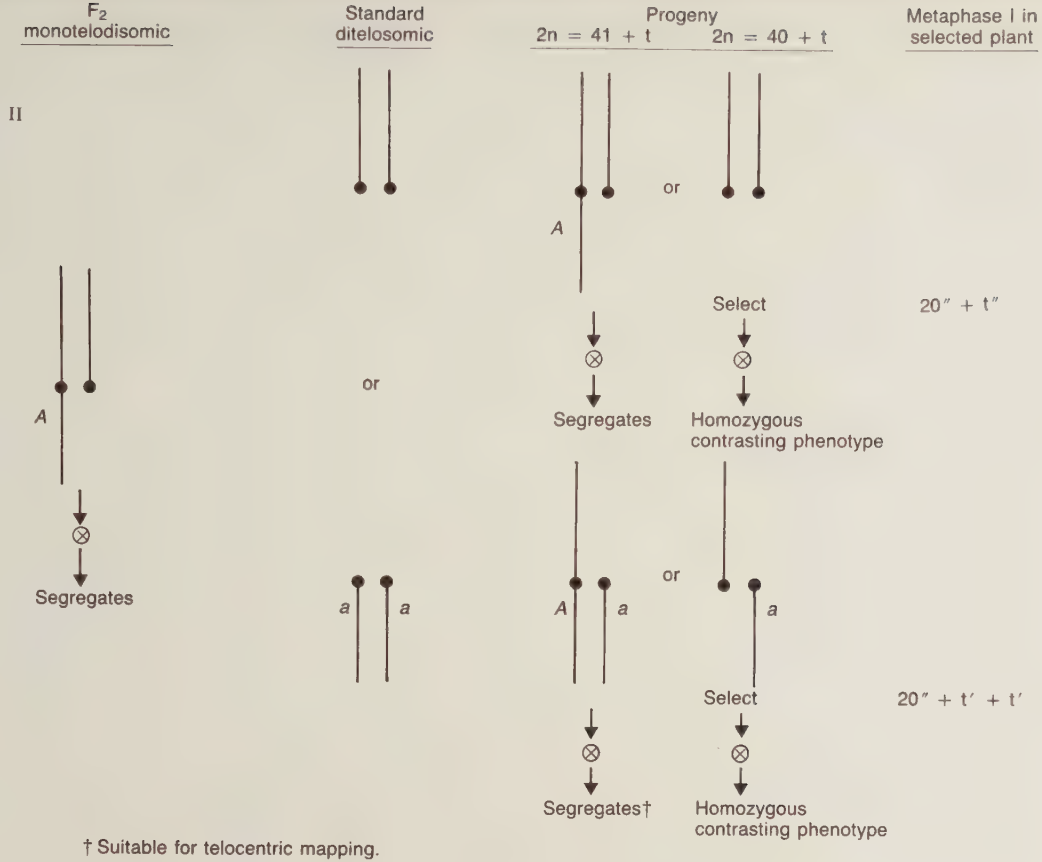


Fig. 5G–2. Possible chromosome arrangements and genetic behavior when a telosome in a monotelodisomic plant is checked with the presumed corresponding standard ditelocentrics. If the unknown telosome is not homologous, the selected plant with two telosomes in the right column will always be 19″+1t″+1t″.



† Suitable for telocentric mapping.

Fig. 5G–2. Continued.

in the monotelodisomic, while progeny-testing the monotelodisomic will establish whether it is homozygous, and therefore whether the telosome carries the gene of interest. Figure 5G–2 outlines some of the possibilities that may arise from such tests. Progeny analysis should furnish supporting data for the original monosomic analysis.

The analysis of spontaneously derived telosomes permits the chromosome arm location of genes located close to the centromere. For example, McIntosh (1980) showed that *Sr14* was located in chromosome 1BL, although no recombinant progeny was obtained from attempted telocentric mapping, using an appropriately constructed heterozygous monotelodisomic.

McIntosh (1972) described another means of detecting marked telocentric chromosomes. Unpaired chromosomes frequently undergo misdivision (Sears 1952) and certain chromosomes, especially misdivision products, are prone to somatic chromosome loss. Where such chromosomes carry marker genes such as those affecting chlorophyll characters (Steinitz-Sears, 1966; McIntosh and Baker, 1968a) or disease resistance (The and Baker, 1973), somatic chromosome loss is reflected in chimeric phenotypes. McIntosh (1972) recovered a 6AL telosome carrying *Sr13* from such a chimera. However, chimeras are not always the consequence of somatic loss of telocentric chromosomes. While isochromosomes may be involved, these are not as useful in further cytogenetic manipulations as telochromosomes. Somatic loss of marked monosomic chromosomes also occurs (McIntosh, unpublished). Chimerism is often observed on seedling leaves, but the recovery of marked telosomes is dependent on continuation of the tissue carrying them until the reproductive stage.

All possible telocentric chromosomes are available in Chinese Spring wheat. Where not originally isolated in that cultivar (e.g., 2BS, 5DS, 6AL, 7DL), they were converted to Chinese Spring by backcrossing (Sears, unpublished). In his original proposals for telocentric mapping, Sears (1966a) emphasized testcross methods involving minimal cytology. This resulted in recombination values with high standard errors. Later studies outlined the need to obtain maximum information from all individuals tested and to progeny-test when required, the analysis of self-pollinated populations (Driscoll, 1966), and the advantages of recovering rare recombinational products for later confirmation and use. The methods are based on general principles for genetic linkage estimation, but modified in the case of selfed populations to allow for estimation of female and male gametic transmission rates for the telosome.

Figure 5G–3 shows the possible orientations of two alleles with respect to a pair of homologues consisting of a normal and a telocentric chromosome. These individuals can be testcrossed as either male (as in Sears, 1966a) or female parents. Cytological examination of all progeny in order to detect those individuals with the telocentric permits construction of the following matrix for recombination value and frequencies using Fig. 5G–3, example (1):

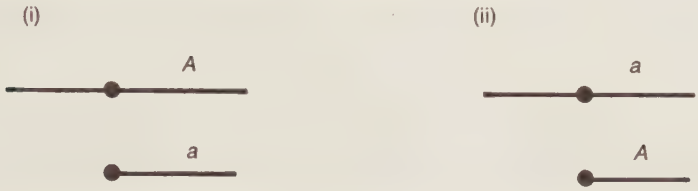


Fig. 5G–3. Orientations of contrasting alleles in a monotelodisomic heterozygote when the locus is present in the homologous chromosome arms.

Phenotype	$2n=42$	Observed frequency	$2n=41+t$	Observed frequency
Aa	$\frac{1}{2}(1-p)$	a	$\frac{1}{2}p$	c
aa	$\frac{1}{2}p$	b	$\frac{1}{2}(1-p)$	d

As with conventional genetic mapping

$$p = (b+c)/N \qquad [10]$$

and

$$s_p = (p(1-p)/N)^{1/2} \qquad [11]$$

The respective gametic transmission rates for the telosome can be easily calculated as:

$$(c+d)/N$$

With selfing, estimates of three parameters are required; namely, the male and female transmission rates for the telosome (x and y, respectively) and the recombination value, p.

The male and female transmission rates for the normal homologue will be $(1-x)$ and $(1-y)$, respectively; hence the ensuing F_2 zygotic frequencies will be

$2n=42$	$(1-x)(1-y)$
$2n=41+t$	$x(1-y) + y(1-x)$
$2n=40+2t$	xy

If telosome transmission through the female is unbiased, i.e., $y=\frac{1}{2}$, the corresponding phenotypic proportions will be:

$2n=42$	$1/2(1-x)$
$2n=41+t$	$1/2x + 1/2(1-x) = 1/2$
$2n=40+2t$	$1/2x$

Hence the ratio $(2n=42 + 2n=40+2t)$: $(2n=41+t) = 1:1$ and the ratio

$(2n=42) : (2n=40+2t) = (1-x) : x$. The latter will be 1:1 only if the male gametic transmission rates for both homologues are equal, i.e., $x = \frac{1}{2}$.

Table 5G–3 presents an example of F_2 data expected for a monotelodisomic *Aa* F_1, with the dominant allele *A* present in the pairing arm of the entire homologue. The expected proportions can be written with $y = \frac{1}{2}$, provided $a+b+e+f : c+d = 1:1$.

Using the phenotypic frequencies from Table 5G–3, the following maximum likelihood equation can be derived:

$$a\left(\frac{2p}{1-p^2}\right) + b\left(\frac{2}{p}\right) - c\left(\frac{1-2p}{1-p+p^2}\right) + d\left(\frac{1-2p}{p(1-p)}\right) + e\left(\frac{2(1-p)}{p(2-p)}\right) - f\left(\frac{2}{1-p}\right) = 0 \quad [12]$$

While it is not required for estimating p, an estimate of the male transmission rate is needed for calculation of s_p from the information values listed in Table 5G–3.

Male transmission rate of the telosome is:

$$x = e+f/[(a+b)+(e+f)] \quad [13]$$

and

$$s_x = (2x(1-x)/N)^{1/2} \quad [14]$$

Table 5G–3. Expected proportion and observed frequencies of F_2 individuals in the progeny of an *Aa* monotelodisomic individual with *A* present in the entire homologue and *a* present in the telosome (p = linkage of *A/a* with centromere. x = male transmission of the telosome).

Chromosome number	Phenotype	Expected proportion	Observed number	i
42	A	$\frac{1}{2}(1-x)(1-p^2)$	a	$\frac{2(1-x)p^2}{1-p^2}$
	a	$\frac{1}{2}(1-x)p^2$	b	$2(1-x)$
41+t	A	$\frac{1}{2}(1-p+p^2)$	c	$\frac{(1-2p)^2}{2(1-p+p^2)}$
	a	$\frac{1}{2}(p-p^2)$	d	$\frac{(1-2p)^2}{2x(1-p)^2}$
40+2t	A	$\frac{1}{2}xp(2-p)$	e	$\frac{2(p-p^2)}{2p-p^2}$
	a	$\frac{1}{2}x(1-2p+p^2)$	f	$2x$
		Total	N	Σi

then

$$s_p = (1/I)^{1/2} = (1/N\Sigma i)^{1/2} \quad [15]$$

Westcott et al. (1978) also considered corresponding examples where *A* is located in the telosome and where there is no dominance, or alternatively where genotypes have been established by progeny testing.

When the arm location of the locus *A/a* is unknown, a failure to obtain recombinant offspring indicates either that the locus is present in the other arm, or that, if present in the paired arm, it is so close to the centromere that recombination is unlikely. At least the data do confirm that *A/a* is present in the chromosome being analyzed. To resolve the alternative possibilities, telocentric mapping can be performed using the telocentric for the opposite arm, or a search can be made for a telocentric product among progenies of a plant monosomic for the chromosome carrying *A*. McIntosh (1980) failed to obtain recombination between *Sr14* and the centromere in monotelodisomic 1BL plants, but showed that a presumably 1BL mono- (and di-) telocentric derivative from a monosomic 1B plant possessed *Sr14*, hence indicating the presence of *Sr14* near the centromere in chromosome 1BL.

On the other hand, if genetic independence with respect to the centromere is obtained, the data do not necessarily confirm that a locus is present in the chromosome under test, since its presence in any other chromosome will give similar results. Here, if telocentric mapping using the opposite chromosome arm should fail to give recombination, it would provide proof for the presence of the gene in the first arm.

Results suggesting extremely small linkage values must be treated with caution as the researcher must be alert to the possibility of both technical and biological errors. Every attempt should be made to recover progeny from rare recombinational events and, where possible, to demonstrate their unique characteristics. McIntosh and Baker (1968b) concluded that *D1*, a complementary gene for grass-clump dwarfness, was located near the centromere in chromosome 2DL on the basis that a dwarf putative recombinant plant with a telocentric chromosome occurred among the testcross progeny. Since the dwarf condition was lethal, no progeny were recovered for confirmatory analysis. Further linkage data later furnished by R.J. Metzger (Oregon State University, personal communication, 1970) suggested that *D1* was unlikely to be located near the centromere in 2DL.

Another study, by Williams and Maan (1973), indicated that *Sr19* could be situated near the centromere in either 2BL or 2BS, since putative recombinants were identified in tests involving both chromosome arms. One possibility for such ambiguity is technical error arising from incorrect identification of a telosome, or from incorrect judgment of a phenotype. In addition, there is no doubt that in rare instances, the telosome and

its normal homologue, or any other chromosome pair, may fail to synapse, with the consequence that misdivision telocentric products may be interpreted as recombinants. The resultant telosome may be either a marked telosome carrying *A* but not derived by recombination, or a telosome, of presumably similar size, involving an unrelated chromosome while *A* remains in its unchanged entire chromosome. Such biological errors regularly occur at low frequencies, but will result in incorrect conclusions only when the locus is not in the homologous chromosome arm, or when the recombination value is very small. Cytological checks of telosomes in rare putative recombinants will provide explanations for certain errors, but will not resolve chromosome misdivision vs. recombination in those situations where the gene is located near the centromere in the chromosome arm being considered.

Some, especially small, telocentric chromosomes may not undergo regular synapsis with normal homologues, or at least may appear to be unpaired at metaphase I. By collecting pairing data at diakinesis, Fu and Sears (1973) showed that desynapsis following opportunities for recombination, rather than asynapsis and hence no opportunity for recombination, may be involved. If the degree of asynapsis can be determined and if an equivalent lack of pairing is not expected for normally paired entire homologues, appropriate corrections can be applied to estimated recombination values. A consequence of unpaired chromosomes in wheat is the production of unbalanced gametes, which will be reflected in progenies with chromosome numbers other than 42. While certain such progenies can be allocated positively to recombinant and nonrecombinant classes, others cannot. An alternative procedure is to include only progenies with 42 chromosomes in subsequent data analyses.

Several well-documented genes in wheat are situated in alien chromosome segments; these segments are usually located terminally rather than being intercalary. Mapping of alien genes actually involves mapping of break-points, since recombination within translocated alien segments is unlikely to occur. Moreover, it is possible that linkage blocks may occur in chromosome segments usually considered closely related to normal wheat. For example, *Sr36* (*SrTt1*) in certain *T. timopheevii* derivatives behaved as if it were an allele of *Sr9* (McIntosh and Luig, 1973); however, they obtained a rare *Sr36 Sr9e* recombinant. Subsequent studies with this recombinant indicated not only a new recombination value of approximately 20%, but also that *Sr36* and *Sr9e* were located in different arms of chromosome 2B (Gyarfas, 1978).

Baker and McIntosh (1973) stressed the usefulness of conserving marked telocentric chromosomes deriving from chromosome misdivision and/or recombination. Such stocks are not only ideal for verification of earlier work, but are also of use in future linkage studies.

5G–3 CHROMOSOME MAPS

Recombination data can be used to construct genetic maps. While considerable linkage data for wheat have been published, only in a few

instances have attempts been made to convert the recombination values to map units (centimorgans [cM]). Recombination fractions and map distances correspond only over relatively short recombinational distances. As genetic distance increases, the probability of a second (and correcting) recombination also increases, hence the measured recombination for two loci is less than would be apparent if a third intervening locus were present. Various mapping functions have been suggested to permit single recombination fractions to be converted to map distances. The simplest and probably most general is that of Kosambi (Bailey, 1961):

$$x = 25 \log_n [(1+2y)/(1-2y)] \qquad [16]$$

where x is the map distance (cM) corresponding to the recombination fraction, y. Using this mapping function, various recombination fractions convert to map distances (cM) as follows:

Recombination fraction	cM	Recombination fraction	cM
0.05	5	0.3	34.7
0.1	10.1	0.4	54.9
0.2	21.1	0.45	73.6

5G–4 CONCLUDING REMARKS

Cytogenetic analyses of wheat do not necessarily simplify problems of genetic analysis. Because of the large number of chromosomes and the paucity of known gene locations, aneuploid analysis is in the mid-1980s the most direct approach to identification of gene:chromosome relationships. Ideally, a hypothesis as to the genetic basis for a particular phenotype is established prior to attempted chromosome location; then the data of the cytogenetic analysis should permit statistical identification of the chromosome(s) involved as well as permitting tests of the hypothesis. Further cytogenetic manipulations, including telocentric mapping, in turn confirm the chromosome locations indicated by statistical analyses. As with conventional genetic analysis, progeny testing may be necessary in situations where phenotypic classification on an individual plant basis is difficult. Moreover, progeny testing enables more complete genetic classification and usually results in linkage values with smaller standard errors. More importantly, it permits further examination of recombinant progenies (which, especially if rare, should be conserved for future reference and use).

If the character of interest has a complex genetic basis, chromosome substitution may enable separation of genetic components which can be analyzed separately. However, the method of analysis will vary with the type of character, with the number and dominance of the genes involved, and with the availability and choice of an aneuploid series.

5H Linkage Map of Hexaploid Wheat

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As indicated in the section 5G on gene location and gene mapping, genetic linkage maps in wheat are sparse. The assignment of genes to chromosomes and chromosome arms has been determined mainly by cytogenetic analyses using various aneuploids or aneuploid procedures.

References to reports on genes and linkage values can be found in publications by McIntosh (1973, 1983) and in: annual supplements published in the Annual Wheat Newsletter, sponsored by the National Wheat Improvement Committee, USA; the Cereal Research Communications, published by the Cereal Research Institute, Szeged, Hungary; and the Wheat Information Service, published by the Kihara Institute for Biological Research, Yokohama, Japan.

5H–1 LINKAGE MAP OF WHEAT

The maps presented herein for the seven groups and three genomes of wheat (*Triticum aestivum* L.: 2n=42) require the following comments:

—Homoeologous chromosome arms are oriented in the same direction.

—Chromosome arms are designated by (i) L = long and S = short; (ii) when length is indistinguishable, by α and β; or (iii) according to homoeology, with p corresponding to short arms and q to long, where there is no conflict with homoeology.

—The centromere is given the value 0, and all values shown on the chromosome are relative to the centromere. Other genes given on the map indicate likely relative positions.

—"†" refers to genes transferred from alien species.

—"‡" indicates that the differing arm locations are unresolved.

—In linkage estimates, I = genetic independence.

Symbols used in the linkage maps are listed in Table 5H–1.

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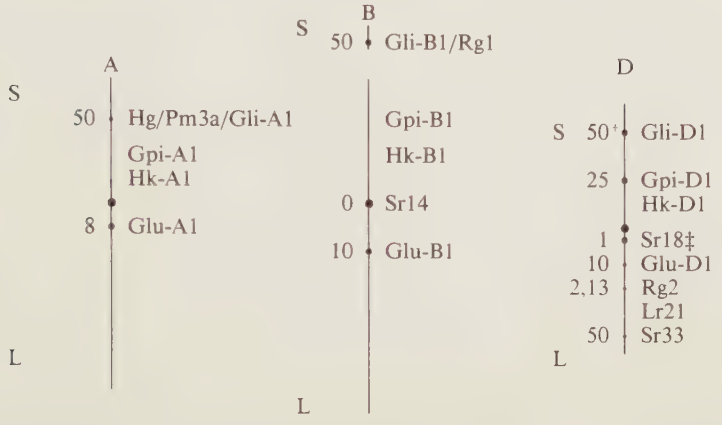
Wheat and Wheat Improvement—Agronomy Monograph no. 13. (2nd Edition).

Table 5H-1. Symbols in Linkage Map of Wheat

Acph	Acid phosphatase
Adh	Alcohol dehydrogenase
Amp	Aminopeptidase
Amy	Amylase
B	Inhibitor of awns
Bg	Black glume color
Bs	Inhibitor of basal sterility in speltoids
Bt	Reaction to *Tilletia* spp.
C	Club spike shape
Ch	Hybrid chlorosis
Cn	Chlorina
Co	Corroded
Cre	Reaction to *Heterodera avenae*
Crr	Reaction to *Cochliobolus sativus*
D	Grass clump dwarfness
Ep	Endopeptidase
Est	Esterase
Gai	Gibberellic acid insensitivity
Gli	Gliadin
Glu	Glutenin
Got	Glutamate oxaloacetate transaminase
Gpi	Glucose phosphate isomerase
H	Reaction to *Mayetiola destructor*
Ha	Grain hardness
Hd	Hooded (awns)
Hg	Hairy glume
Hk	Hexokinase
Hl	Hairy leaf
Hn	Hairy node
Hp	Hairy peduncle
Ki	Pollen killer
Kr	Crossability with rye
Lg	Liguleless
Lpx	Lipoxygenase
Lr	Reaction to *Puccinia recondita*
Ltp	Low temperature pairing
Ms	Male sterility
Ne	Hybrid necrosis
Pbc	Pseudo-black chaff
Pc	Purple culm
Pde	Phosphodiesterase
Ph	Pairing homoeologous
Pln	Sterol esterification
Pm	Reaction to *Eryisyphe graminis*
Ppd	Response to photoperiod
Pro	Protein in seeds
Pur	Lipopurothionin
Q	Spelt factor
R	Red grain color
Ra	Red auricles
Rc	Red coleoptiles
Rf	Restorer for cytoplasmic male sterility
Rg	Red glume color
Rht	Reduced height
S	Sphaerococcum factor
Skdh	Shikimate dehydrogenase
Sr	Reaction to *Puccinia graminis*
Tg	Tenacious glumes
Tpi	Triosephosphate isomerase
V	Virescent
Vrn	Response to vernalization
W	Waxiness
Yr	Response to *Puccinia striiformis*

(continued on next page)

Group 1



S arm: Bg
Lr10

L arm: Pur-A1

Unknown: Rf1

Linkage estimates:
Gli-A1 - Glu-A1 : 66
Hg - Bg : 12
Hg - Pm3a : 1,5

S arm: Yr9†/Lr26†/
Sr31†/Pm8†
Yr10

L arm: Pur-B1

Unknown: Bt4
Bt5
Bt6
Rf3

Linkage estimates:
Bt4 - Bt5 : 30
Bt4 - Bt6 : 15
Gli-B1 - Glu-B1 : 66
Rg1 - Bt4 : 14,23
Rg1 - Bt5 : I
Rg1 - Yr10 : 2
Sr14 - Rg1 : I

S arm: Hk-D1 proximal to
Gpi-D1

L arm: Lr21
Pur-D1

Linkage estimates:
Gli-D1 - Glu-D1 : 48
Gli-D1 - Gpi-D1 : 35
Gpi-D1 - Glu-D1 : 36
Rg2 - Lr21 : 2,3,10
Rg2 - Sr33 : 35
Sr33 - Lr21 : 21

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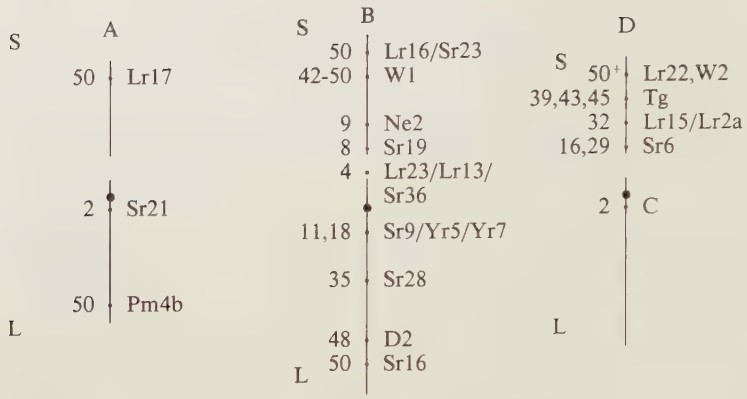
Group 2



Unknown: Ch1
Lr11
ppd3
Rht7
Sr32†
Yr1

Linkage estimates:
Lr17 - Lr11 : I
Sr21 - Pm4b : 38

S arm: ppd2

L arm: Sr20

Unknown: Bt1
Cre
Lg1
Pm6
Sr32
Vrn2

Linkage estimates:
Lr23/Sr36-Sr9b/Sr9e : 20
Lr23 - Sr9b : 22,24,30
Lr23 - Sr28 : 29
Ne2 - D2 : 34
Sr9b - Sr28 : 17
Sr9b - D2 : 42
Sr9b - Sr16 : I
Sr9a - Sr16 : I
Sr9a - Sr19 : <1,25
Sr9d - Sr19 : 24
Sr9d - Sr20 : I
Sr9g - Sr16 : 35
Sr9g - Yr7 : 2
Sr19 - Sr20 : I
Sr20 - Sr16 : I
Sr28 - Sr16 : 29,38
Sr36 - Sr9d : 24

Unknown: Bt7
D4
Lg2
ppd1
Ra
Sr32
Yr8/Sr34†

Linkage estimates:
C - D1 : 37
C - D4 : I
D1 - D4 : 12
Lr2a - C : 10
Lr15 - Lr2 : 0
Lr22 - Tg : 6,21,32,42
Lr22b - Tg : 12
Lr22b - W2 : 11,15,18,42
Sr6 - Lr2a : 1
Sr6 - Ra : 0
Sr6 - C : 18,19,33
Sr6 - Lr15 : <1
W2 - Tg : 15,21,22,28

(continued on next page)

Group 3

S arm: Est-A1
Tpi-A1

L arm: Got-A3
R2

Unknown: Pde-A1
Pde-A3
Sr27†
v2

Linkage estimates:
Sr35 - R2 : 1

S arm: Est-B1
Hk-B2
Lr27
Sr2/Pbc
Sr12
Tpi-B1

L arm: Got-B3

Unknown: Pde-B1
Pde-B3
R3

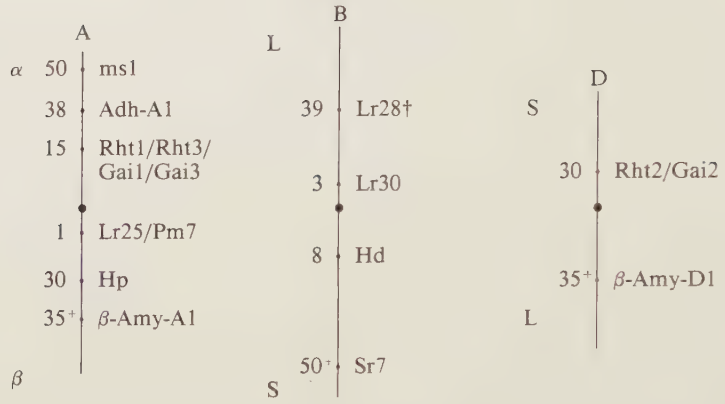
S arm: Est-D1
Pde-D1
Pde-D3
ph2
Tpi-D1

L arm: Got-D3
Sr24/Lr24†

Unknown: v3

(continued on next page)

Group 4



α arm: Lpx-A1

β arm: Acph4
Acph8
Sr37

Unknown: Hl
Lr12
Lr16

Linkage estimates:
Lr12 - Lr16 : I
Lr16 - Sr23 : <1
ms1b - Lr25 : 34
ms1c - Lr25 : 20

L arm: Adh-B1
D3
Lpx-B1

S arm: Acph2
Acph3

Linkage estimates:
Sr7a - Hd : I

S arm: Adh-D1
Lpx-D1

L arm: Acph5
Acph6

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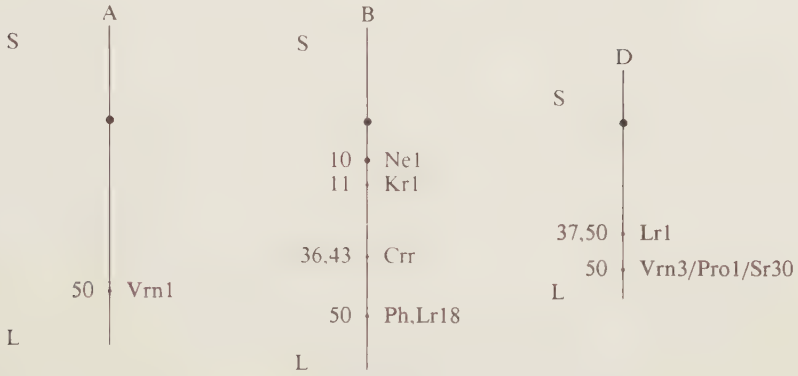
Group 5



S arm: Skdh-A1

L arm: Adh-A2
β-Amy-A2
B1
Hn
Kr2
Lpx-A2
q

Unknown: H3
H6
H9
H10

Linkage estimates:

β-Amy-A2 - B1 : 2
B1 - Hn : 5
H3 - H6 : 9
H3 - H9 : 16
H6 - H9 : 2
H9 - H10 : 36,I
q - B1 : 30,33,37,41
q - Hn : 36

Gene order:

β-Amy-A2 - B1 - Hn - Q - Vrn1

S arm: Skdh-B1

L arm: Adh-B2
Lpx-B2

S arm: Ha
Pm2
Pro2
Skdh-D1

L arm: Adh-D2
Lpx-D2

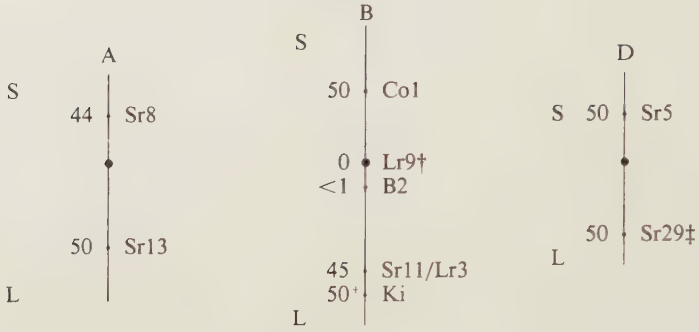
Unknown: Bs
Ltp

Linkage estimates:

Lr1 - Pm2 : I
Sr30 - Lr1 : I
Sr30 - Pm2 : I

(continued on next page)

Group 6



S arm: Amp-A1
Got-A1

L arm: Est-A2
Got-A2
Sr26†

S arm: Amp-B1
Got-B1

L arm: Est-B2
Got-B2

Unknown: Rf4

Linkage estimates:
B2 - Lr9 : 4
B2 - Sr11 : 43,47
Ki - Sr11 : 9
Ki - Lr3 : 12
Sr11 - Lr9 : v.small
Sr11 - Lr3 : 0,22

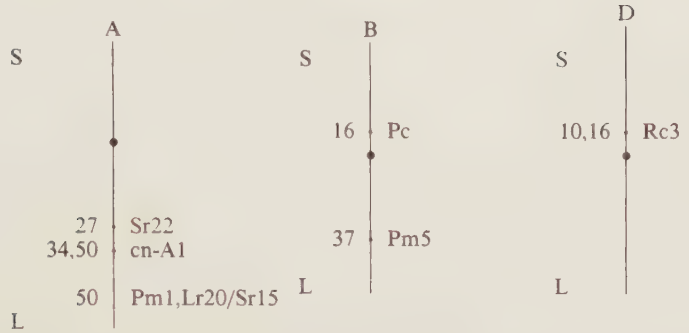
S arm: Amp-D1
Got-D1
Sr29‡

L arm: Co2
Est-D2
Got-D2

Unknown: Rf5

(continued on next page)

Group 7



L arm: Ep-A1
Pm9

Unknown: Rc1

Linkage estimates:
Sr22 - cn-A1 : 2
Sr22 - Pm1 : 41
cn-A1 - Pm1 : 40

S arm: Rc2
Vrn5
Yr6

L arm: α-Amy
Ep1
Ep-B1
cn-B1
Lr14
Sr17

Unknown: Yr2

Linkage estimates:
Lr14 - Pc : 44
Lr14 - Pm5 : 20,28
Lr14a - Sr17 : 18
Pc - Vrn5 : 26
Pm5 - Vrn5 : 39
Sr17 - Pm5 : 3,6

S arm: Lr29†
P1n

L arm: cn-D1
Ep-D1
Sr25/Lr19†

Unknown: Rf2

Linkage estimates:
Lr19 - cn-D1 : 0

REFERENCES

Adams, J., and E.D. Rothman. 1982. Estimation of phylogenetic relationships from DNA restriction patterns and selection of endonuclease cleavage sites. Proc. Natl. Acad. Sci. USA 79:3560–3564.

Ainsworth, C.C. 1983. The genetic control of hexokinase isozymes in wheat. Genet. Res. Camb. 42:219–227.

----, and M.D. Gale. 1987. Enzyme structural genes and their exploitation in wheat breeding and genetics. p. 53–82. *In* J.E. Kruger et al. (ed.) Enzymes and their role in cereal technology. Am. Assoc. Cereal Chemists, Minneapolis.

----, ----, and S. Baird. 1983. The genetics of α-amylase isozymes in wheat. I. Allelic variation among hexaploid varieties and intrachromosomal gene locations. Theor. Appl. Genet. 66:39–49.

----, ----, and ----. 1984a. The genetic control of grain esterases in hexaploid wheat. I. Allelic variation. Theor. Appl. Genet. 68:219–226.

----, H.M. Johnson, E.A. Jackson, T.E. Miller, and M.D. Gale. 1984b. The chromosomal locations of leaf peroxidase genes in hexaploid wheat, rye, and barley. Theor. Appl. Genet. 69:205–210.

----, T.E. Miller, and M.D. Gale. 1986. The genetic control of grain esterases in hexaploid wheat. II. Homoeologous loci in related species. Theor. Appl. Genet. 72:219–225.

Akam, M. 1983. Decoding the *Drosophila* complexes. Trends Biochem. Sci. (Pers. Ed.) 8:173–177.

Albini, S.M., G.H. Jones, and B.M.N. Wallace. 1984. A method for preparing two-dimensional surface-spreads of synaptonemal complexes from plant meiocytes for light and electron microscopy. Exp. Cell Res. 152:280–285.

Allan, R.E., and O.A. Vogel. 1960. F_1 monosomic analysis involving a smooth awn durum wheat. Wheat Inf. Serv. 11:3–4.

Allard, R.W. 1956. Formulas and tables to facilitate the calculation of recombination values in heredity. Hilgardia 24:235–278.

Alonso, L.C., and G. Kimber. 1981. The analysis of meiosis in hybrids. II. Triploid hybrids. Can. J. Genet. Cytol. 23:221–234.

----, and ----. 1983a. A study of genomic relationships in wheat based on telocentric chromosome pairing, I. Z. Pflanzenzuecht. 90:23–31.

----, and ----. 1983b. A study of genomic relationships in wheat based on telocentric chromosome pairing, II. Z. Pflanzenzuecht. 90:273–284.

Anderson, L.M., and C.J. Driscoll. 1967. The production and breeding behaviour of a monosomic alien substitution line. Can. J. Genet. Cytol. 9:399–403.

Anderson, O.D., J.C. Litts, M.-F.Gautier, and F.C. Greene. 1984. Nucleic acid sequence and chromosome assignment of a wheat storage protein gene. Nucleic Acids Res. 12:8129–8144.

Aniol, A. 1974. A serological investigation of wheat evolution. Z. Pflanzenzuecht. 73:194–203.

Appels, R. 1982. The molecular cytology of wheat-rye hybrids. Int. Rev. Cytol. 80:93–132.

----. 1983. Chromosome structure in cereals: the analysis of regions containing repeated sequence DNA and its application to the detection of alien chromosomes introduced into wheat. p. 229–256. *In* T. Kosuge et al. (ed.) Genetic engineering of plants: An agricultural perspective. Plenum Press, New York.

----, E.S. Dennis, D.R. Smyth, and W.J. Peacock. 1981. Two repeated DNA sequences from the heterochromatic regions of rye (*Secale cereale*) chromosomes. Chromosoma 84:265–277.

----, C.J. Driscoll, and W.J. Peacock. 1978. Heterochromatin and highly repeated DNA sequences in rye (*Secale cereale*). Chromosoma 70:67–89.

----, and J. Dvořák. 1982a. The wheat ribosomal DNA spacer region: Its structure and variation in populations and among species. Theor. Appl. Genet. 63:337–348.

----, and ----. 1982b. Relative rates of divergence of spacer and gene sequences within the rDNA region of species in the *Triticeae*: Implications for the maintenance of homogeneity of a repeated gene family. Theor. Appl. Genet. 63:361–365.

----, W.L. Gerlach, E.S. Dennis, A. Swift, and W.J. Peacock. 1980. Molecular and chromosomal organization of DNA sequences coding for the ribosomal RNAs of cereals. Chromosoma 78:293–311.

----, J.P. Gustafson, and C.E. May. 1982. Structural variation in the heterochromatin of rye chromosomes in triticales. Theor. Appl. Genet. 63:235–244.

----, and R.J. Honeycutt. 1986. rDNA : Evolution over a billion years. p. 81–136. *In* S.K. Dutta (ed.) DNA systematics, Vol. 2. CRC Press, Boca Raton, FL.

----, and L. Moran. 1984. Molecular analysis of alien chromatin introduced into wheat. p. 529–557. *In* J.P. Gustafson (ed.) Proc. 16th Stadler Symp., Columbia, MO. 19–21 March. University of Missouri, Columbia.

Autran, J.-C. 1981. Recent data on the biochemical basis of durum wheat quality. p. 257–273. *In* G. Charalambous and G.E. Inglett (ed.) The quality of foods and beverages. Chemistry and Technology, Vol. 1. Academic Press, New York.

----, and A. Bourdet. 1975. L'identification des variétés de blé: Établissement d'un tableau général de détermination fondé sur le diagramme électrophorétique des gliadines du grain. Ann. Amélior. Plant. 25:277–301.

Avivi, L., and M. Feldman. 1980. Arrangement of chromosomes in the interphase nucleus of plants. Hum. Genet. 55:281–295.

Bailey, N.T.J. 1961. Introduction to the mathematical theory of genetic linkage. Oxford University Press, London.

Baker, E.P., and R.A. McIntosh. 1973. Utilization of marked telocentric chromosomes in more efficient genetic analysis. p. 635–636. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Barber, H.N., C.J. Driscoll, P.M. Long, and R.S. Vickery. 1968. Protein genetics of wheat and homoeologous relationships of chromosomes. Nature (London) 218:450–452.

----, ----, ----, and ----. 1969. Gene similarity of the *Triticinae* and the study of segmental interchanges. Nature (London) 222:897–898.

Barciszewska, M., G. Dirheimer, and G. Keith. 1983. The nucleotide sequence of methionine elongator tRNA from wheat germ. Biochem. Biophys. Res. Commun. 114:1161–1168.

Batey, I. 1984. Wheat varietal identification by rapid ion-exchange chromatography of gliadins. J. Cereal Sci. 2:241–248.

Bazetoux, S., L. Jouanin, and T. Huguet. 1978. Characterisation of inverted repeated sequences in wheat nuclear DNA. Nucleic Acids Res. 5:751–769.

Beckwith, A.C., and D.C. Heiner. 1966. An immunological study of wheat gluten proteins and derivatives. Arch. Biochem. Biophys. 117:239–247.

Bedbrook, J., J. Jones, M. O'Dell, R.D. Thompson, and R.B. Flavell. 1980. A molecular description of telomeric heterochromatin in *Secale* species. Cell 19:545–560.

Bendich, A.J., and B.J. McCarthy. 1970a. DNA comparisons among barley, oats, rye and wheat. Genetics 65:545–565.

----, and ----. 1970b. DNA comparisons among some biotypes of wheat. Genetics 65:567–573.

Benito, C., A.M. Figueiras, and M.T. Gonzalez-Jaen. 1984. Phosphogluco mutase - a biochemical marker for group 4 chromosomes in the Triticinae. Theor. Appl. Genet. 68:555–557.

----, ----, ----, and J. Salinas. 1985. Biochemical evidence of homoeology between wheat and barley chromosomes. Z. Pflanzenzuecht. 94:307–320.

----, and M. Perez de la Vega. 1979. The chromosomal location of peroxidase isozymes of the wheat kernel. Theor. Appl. Genet. 55:73–76.

----, and J. Salinas. 1983. The chromosomal location of malate dehydrogenase isozymes in hexaploid wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 64:255–258.

Bennett, M.D. 1972. Nuclear DNA content and minimum generation time in herbaceous plants. Proc. R. Soc. London Ser. B 181:109–135.

----. 1983. The spatial distribution of chromosomes. p. 71–79. *In* P.E. Brandham and M.D. Bennett (ed.) Kew chromosome conference No. II. George Allen and Unwin, London.

----, J.P. Gustafson, and J.P. Smith. 1977. Variation in nuclear DNA in the genus *Secale*. Chromosoma 61:149–176.

----, and J.B. Smith. 1976. Nuclear DNA amounts in angiosperms. Proc. R. Soc. London Ser. B. 274:227–274.

Bergman, J.W. 1972. Chromosome location of genes controlling esterase and malate dehydrogenase isozymes in *Triticum*. Ph.D. diss. North Dakota State University, Fargo. (Diss. Abstr. Int. Series B Vol. 34:23–B. 1973.)

Bielig, L.M., and C.J. Driscoll. 1973. Release of a series of MAS lines. p. 147–150. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Bietz, J.A. 1982. Cereal prolamin evolution and homology revealed by sequence analysis. Biochem. Genet. 20:1039–1053.

----. 1983. Separation of cereal proteins by reversed-phase high-performance liquid chromatography. J. Chromatogr. 255:219–238.

----. 1984. Analysis of wheat gluten proteins by high-performance liquid chromatography, I. Baker's Dig. 58(1):15–17, 20–21, 32.

----. 1985. High-performance liquid chromatography: How proteins look in cereals. Cereal Chem. 62:201–212.

----, and T. Burnouf. 1985. Chromosomal control of wheat gliadin: Analysis by reversed-phase high-performance liquid chromatography. Theor. Appl. Genet. 70:599–608.

----, ----, L.A. Cobb, and J.S. Wall. 1984a. Gliadin analysis by reversed-phase high-performance liquid chromatography: Optimization of extraction conditions. Cereal Chem. 61:124–129.

----, ----, L.A. Cobb, and J.S. Wall. 1984b. Wheat varietal identification and genetic analysis by reversed-phase high-performance liquid chromatography. Cereal Chem. 61:129–135.

----, and L.A. Cobb. 1985. Improved procedures for rapid wheat varietal identification by reversed-phase high-performance liquid chromatography of gliadin. Cereal Chem. 62:332–339.

----, F.R. Huebner, J.E. Sanderson, and J.S. Wall. 1977. Wheat gliadin homology revealed through N-terminal amino acid sequence analysis. Cereal Chem. 54:1070–1083.

----, K.W. Shepherd, and J.S. Wall. 1975. Single-kernel analysis of glutenin: Use in wheat genetics and breeding. Cereal Chem. 52:513–532.

----, and J.S. Wall. 1972. Wheat gluten subunits: Molecular weights determined by sodium dodecyl sulfate-polyacrylamide gel electrophoresis. Cereal Chem. 49:416–430.

----, and ----. 1980. Identity of high molecular weight gliadin and ethanol-soluble glutenin subunits of wheat: Relation to gluten structure. Cereal Chem. 57:415–421.

Bonen, L., and M.W. Gray. 1980. Organisation and expression of the mitochondrial genome of plants. I. The genes for wheat mitochondrial ribosomal and transfer RNA: Evidence for an unusual arrangement. Nucleic Acids Res. 8:319–335.

----, T.Y. Huh, and M.W. Gray. 1980. Can partial methylation explain the complex fragment patterns observed when plant mitochondrial DNA is cleaved with restriction endonucleases? FEBS Lett. 111:340–346.

Bowman, C.M., G. Bonnard, and T.A. Dyer. 1983. Chloroplast DNA variation between species of *Triticum* and *Aegilops*: Location of the variation on the chloroplast genome and its relevance to the inheritance and classification of the cytoplasm. Theor. Appl. Genet. 65:247–262.

----, and T.A. Dyer. 1982. Purification and analysis of DNA from wheat chloroplasts isolated in nonaqueous media. Anal. Biochem. 122:108–118.

----, B. Koller, H. Delius, and T.A. Dyer. 1981. A physical map of wheat chloroplast DNA

showing the location of the structural genes for the ribosomal RNAs and the large subunit of ribulose 1,5-bisphosphate carboxylase. Mol. Gen. Genet. 183:93–101.

Boyd, W.J.R., and J.W. Lee. 1967. The control of wheat gluten synthesis at the genome and chromosome levels. Experientia 23:332–333.

----, ----, and C.W.Wrigley. 1969. The D-genome and the control of wheat gluten synthesis. Experientia 25:317–319.

Bozzini, A., P. Cantagalli, S.E. Piazzi, and S. Sordi. 1970. An immunochemical approach to species relationship in *Triticum* and some related species. Theor. Appl. Genet. 40:300–304.

----, and F. Carluccio. 1973. Comparative monopentaploid analysis of 5A chromosomes of 8 lines of tetraploid wheats and of the hexaploid Chinese Spring. Genet. Agrar. 27:148–163.

----, and B. Giorgi. 1971. Genetic analysis of tetraploid and hexaploid wheat by utilization of monopentaploid hybrids. Theor. Appl. Genet. 41:67–74.

Branlard, G. 1983. Correlation between gliadin bands. Theor. Appl. Genet. 64:163–168.

----, and M. Rousset. 1980. Electrophoretical characteristics of gliadins and baking value of bread wheat. Ann. Amelior. Plant. 30:133–149.

Britten, R.J., and D.E. Kohne. 1968. Repeated sequences in DNA. Science 161:529–540.

Broglie, R., G. Coruzzi, G. Lamppa, B. Keith, and N.-H. Chua. 1983. Structural analysis of nuclear genes coding for the precursor to the small subunit of wheat ribulose-1,5-bisphosphate carboxylase. Bio/Technology 1:55–61.

Brown, A.H.D. 1980. Genetic basis of alcohol dehydrogenase polymorphism in *Hordeum spontaneum*. J. Hered. 70:127–128.

----. 1983. Barley. p. 57–77. *In* S.D. Tanksley and T.J. Orton (ed.) Isozymes in plant genetics and breeding, Part B. Elsevier Science Publishers B.V., Amsterdam.

----, and J.B. Jacobsen. 1982. Genetic basis and natural variation of α-amylase isozymes in barley. Genet. Res. 40:315–324.

----, and J. Munday. 1982. Population-genetic structure and optimal sampling of land races of barley from Iran. Genetica 58:85–96.

Brown, D.D. 1984. The role of stable complexes that repress and activate eucaryotic genes. Cell 37:359–365.

Brown, J.W.S., and R.B. Flavell. 1981. Fractionation of wheat gliadin and glutenin subunits by two-dimensional electrophoresis and the role of group 6 and group 2 chromosomes in gliadin synthesis. Theor. Appl.Genet. 59:349–359.

----, R.J. Kemble, C.N. Law, and R.B. Flavell. 1979. Control of endosperm proteins in *Triticum aestivum* (var. Chinese Spring) and *Aegilops umbellulata* by homoeologous group 1 chromosomes. Genetics 93:189–200.

----, C.N. Law, A.J. Worland, and R.B. Flavell. 1981. Genetic variation in wheat endosperm proteins: An analysis by two-dimensional electrophoresis using intervarietal chromosomal substitution lines. Theor. Appl. Genet. 59:361–371.

Burnouf, T., and J.A. Bietz. 1984a. Reversed-phase high-performance liquid chromatography of durum wheat gliadins: Relationships to durum wheat quality. J. Cereal Sci. 2:3–14.

----, and ----. 1984b. Reversed-phase high-performance liquid chromatography of reduced glutenin, a disulfide-bonded protein of wheat endosperm. J. Chromatogr. 299:185–199.

----, and ----. 1984c. Reversed-phase high-performance liquid chromatography of gluten proteins from aneuploid lines and related species of wheat. Cereal Foods World 29:506–507. (Abstr.)

----, and ----. 1985. Chromosomal control of glutenin subunits in aneuploid lines of wheat: Analysis by reversed-phase high-performance liquid chromatography. Theor. Appl. Genet. 70:610–619.

----, ----, L.A. Cobb, and J.S. Wall. 1983a. Chromatographie liquide haute performance des gliadines de variétés de blé tendre (*Triticum aestivum* L.) cultivées en France et

possibilités d'identification variétale. C.R. Hebd. Seances Acad. Sci. Ser. D. 297:377–382.

----, and R. Bouriquet. 1980. Glutenin subunits of genetically related European hexaploid wheat cultivars: Their relation to bread-making quality. Theor. Appl. Genet. 58:107–111.

----, ----, and P. Poullard. 1983b. Inheritance of glutenin subunits in F1 seeds of reciprocal crosses between European hexaploid wheat cultivars. Theor. Appl. Genet. 64:103–107.

----, A. Façon-Le Blanc, P. Poullard, and R. Bouriquet. 1981. Étude de la transmission héréditaire des sous-unités de gluténine dans la descendance F_1 et F_2 d'un croisement réciproque entre deux cultivars de blé tendre. Bull. Soc. Bot. Fr. 34:67–74.

Burr, B., S.V. Evola, and F.A. Burr. 1983. The application of restriction fragment length polymorphism to plant breeding. p. 45–61. *In* J.K. Setlow and A. Hollaender (ed.) Genetic engineering—Principles and methods. Vol. V. Plenum Press, New York.

Bushuk, W., and R.R. Zillman. 1978. Wheat cultivar identification by gliadin electrophoregrams. I. Apparatus, method, and nomenclature. Can. J. Plant Sci. 58:505–515.

Caldwell, K.A. 1979. The fractionation and purification of gliadins by hydrophobic interaction chromatography. J. Sci. Food Agric. 30:185–196.

----, and D.D. Kasarda. 1978. Assessment of genomic and species relationships in *Triticum* and *Aegilops* by PAGE and by differential staining of seed albumins and globulins. Theor. Appl. Genet. 52:273–280.

Carrozza, M.L. 1981. Number of sites for ribosomal RNA genes in *Triticum durum*: In situ hybridization on mitotic, meiotic and polytene nuclei. Z. Pflanzenzuecht. 87:300–308.

Cech, T.R. 1983. RNA splicing: Three themes with variations. Cell 34:713–716.

Ceoloni, C., and G. Galili. 1982. Chromosome arm location and mode of expression of a phosphodiesterase gene from diploid wheat *Triticum longissimum*. Cereal Res. Commun. 10:151–157.

Chapman, V., T.E. Miller, and R. Riley. 1976. Equivalence of the A genome of bread wheat and that of *Triticum urartu*. Genet. Res. 27:69–76.

Chen, C.H., and W. Bushuk. 1970. Nature of proteins in *Triticale* and its parental species. III. A comparison of their electrophoretic patterns. Can. J. Plant Sci. 50:25–30.

Chen, P.D., and B.S. Gill. 1983. The origin of chromosome 4A, and genomes B and G of tetraploid wheats. p. 39–48. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University.

Chenicek, K. 1984. Evidence for the genetic control and subcellular locations of aconitase isozymes in Triticeae species. M.S. thesis. Texas A&M University, College Station.

Chojecki, A.J.S., and M.D. Gale. 1982. Genetic control of glucose phosphate isomerase in wheat and related species. Heredity 49:337–347.

----, ----, L.M. Holt, and P.I. Payne. 1983. The intrachromosomal mapping of a glucose phosphate isomerase structural gene, using allelic variation among stocks of Chinese Spring wheat. Genet. Res. 41:221–226.

Chung, K.H., and Y. Pomeranz. 1979. Acid-soluble proteins of wheat flours. II. Binding to hydrophobic gels. Cereal Chem. 56:196–201.

Church, G.M., and W. Gilbert. 1984. Genomic sequencing. Proc. Natl. Acad. Sci. USA 81:1991–1995.

Cole, E.W., J.G. Fullington, and D.D. Kasarda. 1981. Grain protein variability among species of *Triticum* and *Aegilops*: Quantitative SDS-PAGE studies. Theor. Appl. Genet. 60:17–30.

Cooper, D.N. 1983. Eukaryotic DNA methylation. Hum. Genet. 64:315–317.

Cramer, C.L., T.B. Ryder, J.N. Bell, and C.J. Lamb. 1985. Rapid switching of plant gene expression induced by fungal elicitor. Science 227:1240–1243.

Cunningham, R.S., L. Bonen, W.F. Doolittle, and M.W. Gray. 1976. Unique species of 5S, 18S and 26S ribosomal RNA in wheat mitochondria. FEBS Lett. 69:116–122.

Damidaux, R., J.-C. Autran, P. Grignac, and P. Feillet. 1978. Mise en évidence de relations

applicables en sélection entre l'électrophorégramme des gliadines et les propriétés viscoélastiques du gluten de *Triticum durum*. C.R. Hebd. Seances Acad. Sci. Ser. D 287:701–704.

----, ----, ----, and ----. 1980. Déterminisme génétique des constituants gliadines de *Triticum durum* Desf. associés à la qualité culinaire intrinsèque des variétés. C.R. Hebd. Seances Acad. Sci. Ser.D 291:585–588.

Daussant, J., and A. Skakoun. 1983. Immunochemistry of seed proteins. p. 101–133. *In* J. Daussant et al. (ed.) Seed proteins. Academic Press, London.

Davidson, N., J. Widholm, V.S. Nandi, R. Jensen, B.M. Olivera, and T.C. Wang. 1965. Preparation and properties of native crab dAT. Proc. Natl. Acad. Sci. USA 53:111–118.

Dennis, E.S., W.L. Gerlach, and W.J. Peacock. 1980. Identical polypyrimidine–polypurine satellite DNAs in wheat and barley. Heredity 44:349–366.

Dhaliwal, H.S., B.S. Gill, and J.G. Waines. 1977. Analysis of induced homoeologous pairing in a *ph* mutant wheat × rye hybrid. J. Hered. 68:206–209.

Dierks-Ventling, C., and K. Cozens. 1982. Immunochemical crossreactivity between zein, hordein, and gliadin. FEBS Lett. 142:147–150.

Doekes, G.J. 1968. Comparison of wheat varieties by starch-gel electrophoresis of their grain proteins. J. Sci. Food Agric. 19:169–176.

Dover, G., and R. Riley. 1972. The prevention of pairing of homoeologous meiotic chromosomes of wheat by a genetic activity of supernumerary chromosomes of *Aegilops*. Nature (London) 240:159–161.

Driscoll, C.J. 1966. Gene-centromere distances in wheat by aneuploid F2 observations. Genetics 54:131–135.

----. 1972. Genetic suppression of homoeologous chromosome pairing in hexaploid wheat. Can. J. Genet. Cytol. 14:39–42.

----. 1973. Minor genes affecting homoeologous pairing in hybrids between wheat and related genera. Genetics 74:s66. (Abstr.)

----. 1983. Third compendium of wheat–alien chromosome lines. Suppl. Proc. 6th Int. Wheat Genet. Symp.

du Cros, D.L., L.R. Joppa, and C.W. Wrigley. 1983. Two-dimensional analysis of gliadin proteins associated with quality in durum wheat: Chromosomal location of genes for their synthesis. Theor. Appl. Genet. 66:297–302.

----, G.J. Lawrence, D.M. Miskelly, and C.W. Wrigley. 1980. Systematic identification of Australian wheat varieties by laboratory methods. CSIRO Wheat Res. Unit Tech. Publ. 7.

----, and C.W. Wrigley. 1979. Improved electrophoretic methods for identifying cereal varieties. J. Sci. Food Agric. 30:785–794.

----, ----, and R.A. Hare. 1982. Prediction of durum-wheat quality from gliadin-protein composition. Aust. J. Agric. Res. 33:429–442.

Dudock, B.S., and G. Katz. 1969. Large oligonucleotide sequences in wheat germ phenylalanine transfer ribonucleic acid. J. Biol. Chem. 244:3069–3074.

Dvořák, J. 1976. The relationship between the genome of *Triticum urartu* and the A and G genomes of *Triticum aestivum*. Can. J. Genet. Cytol. 18:371–377.

----. 1983. The origin of wheat chromosomes 4A and 4B and their genome reallocation. Can. J. Genet. Cytol. 25:210–214.

----, and R. Appels. 1982. Chromosome and nucleotide sequence differentiation in genomes of polyploid *Triticum* species. Theor. Appl. Genet. 63:349–360.

----, and K.C. Chen. 1984. Distribution of nonstructural variation between wheat cultivars along chromosome arm 6Bp: Evidence from the linkage map and physical map of the arm. Genetics 106:325–333.

----, ----, and B. Giorgi. 1984a. The C-band pattern of a Ph^- mutant of durum wheat. Can. J. Genet. Cytol. 26:360–363.

----, M. Lassner, R.S. Kota, and K.C. Chen. 1984b. Distribution of ribosomal RNA genes

in the genomes of *Triticum speltoides* and *Elytrigia elongata*. Can. J. Genet. Cytol. 26:628–632.

----, P.E. McGuire, and S. Mendlinger. 1984c. Inferred chromosome morphology of the ancestral genome of *Triticum*. Plant Syst. Evol. 144:209–220.

Elton, G.A.H., and J.A.D. Ewart. 1960. Starch-gel electrophoresis of wheat proteins. Nature (London) 187:600–601.

----, and ----. 1962. Starch-gel electrophoresis of cereal proteins. J. Sci. Food Agric. 13:62–72.

----, and ----. 1963. Immunological comparison of cereal proteins. J. Sci. Food Agric. 14:750–758.

----, and ----. 1964. Electrophoretic comparison of cereal proteins. J. Sci. Food Agric. 15:119–126.

----, and ----. 1966. Glutenins and gliadins: Electrophoretic studies. J. Sci. Food Agric. 17:34–38.

Endo, T.R., and B.S. Gill. 1984a. A somatic karyotype, heterochromatin distribution, and nature of chromosome differentiation in common wheat, *Triticum aestivum* L. em. Thell. Chromosoma 89:361–369.

----, and ----. 1984b. The heterochromatin distribution and genome evolution in diploid species of *Elymus* and *Agropyron*. Can. J. Genet. Cytol. 26:669–678.

Esen, A., J.M. Conroy, and S.-Z. Wang. 1983. A simple and rapid dot-immunobinding assay for zein and other prolamins. Anal. Biochem. 132:462–467.

Espinasse, A., and G. Kimber. 1981. The analysis of meiosis in hybrids. IV. Pentaploid hybrids. Can. J. Genet. Cytol. 23:623–638.

Ewart, J.A.D. 1966. Cereal proteins: Immunological studies. J. Sci. Food Agric. 17:279–284.

----. 1969. Comparison of seed proteins of some Gramineae. J. Sci. Food Agric. 20:221–224.

----. 1977. Immunochemistry of wheat proteins. p. 87–116. *In* N. Catsimpoolas (ed.) Immunological aspects of foods. AVI Publishing Co., Westport, CT.

Falconet, D., B. Lejeune, F. Quetier, and M.W. Gray. 1984. Evidence for homologous recombination between repeated sequences containing 18S and 5S ribosomal RNA genes in wheat mitochondrial DNA. EMBO J. 3:297–302.

Fedoroff, N.V. 1984. Transposable genetic elements in maize. Sci. Am. 250:84–98.

----, D.B. Furtek, and O.E. Nelson. 1984. Cloning of the *bronze* locus in maize by a simple and generalizable procedure using the transposable controlling element *Activator* (*Ac*). Proc. Natl. Acad. Sci. USA 81:3825–3829.

Feillet, P., and K. Kobrehel. 1972. Recherche et dosage des produits de blé tendre dans les pâtes alimentaires par électrophorèse des protéines solubles. Ann. Technol. Agric. 21:17–24.

Feldman, M. 1965a. Further evidence for natural hybridization between tetraploid species of *Aegilops* section *Pleionathera*. Evolution 19:162–174.

----. 1965b. Fertility of interspecific F_1 hybrids and hybrid derivatives involving tetraploid species of *Aegilops* section *Pleionathera*. Evolution 19:556–562.

----. 1965c. Chromosome pairing between differential genomes in hybrids of tetraploid *Aegilops* species. Evolution 19:563–568.

----. 1966a. The effect of chromosomes 5B, 5D, and 5A on chromosomal pairing in *Triticum aestivum*. Proc. Natl. Acad. Sci. USA 55:1447–1453.

----. 1966b. Identification of unpaired chromosomes in F1 hybrids involving *Triticum aestivum* and *T. timopheevii*. Can. J. Genet. Cytol. 8:144–157.

----. 1968. Regulation of somatic association and meiotic pairing in common wheat. p. 31–40. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Canberra, Australia. 5–9 August. Australian Academy of Science, Canberra.

----. 1979. New evidence on the origin of the B genome of wheat. p. 120–132. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Ind. Soc. Genet. Plant Breeding, Indian Agric. Res. Inst., New Delhi.

----, and M. Kislev. 1977. *Aegilops searsii*, a new species of section *Sitopsis (Platystachys)*. Isr. J. Bot. 26:190–201.

----, and T. Mello-Sampayo. 1967. Suppression of homoeologous pairing in hybrids of polyploid wheats × *Triticum speltoides*. Can. J. Genet. Cytol. 9:307–313.

Ferrer, E., J.M. Gonzalez, and N. Jouve. 1984. Identification of C-banded chromosomes in meiosis of common wheat, *T. aestivum* L. Theor. Appl. Genet. 67:257–262.

Finch, J.T., and A. Klug. 1976. Solenoidal model for superstructure in chromatin. Proc. Natl. Acad. Sci. USA 73:1897–1901.

----, L.C. Lutter, D. Rhodes, R.S. Brown, B.R. Rushton, M. Levitt, and A. Klug. 1977. Structure of nucleosome core particles of chromatin. Nature (London) 269:29–36.

Fitch, W.M. 1970. Distinguishing homologous from analogous proteins. Syst. Zoo. 19:99–113.

----, and E. Margoliash. 1970. The usefulness of amino acid and nucleotide sequences in evolutionary studies. Evol. Biology 4:67–109.

Flavell, R.B. 1982a. Sequence amplification, deletion and rearrangement: Major sources of variation during species divergence. p. 301–323. *In* G.A. Dover and R.B. Flavell (ed.) Genome evolution. Academic Press, London.

----. 1982b. Chromosomal DNA sequences and their organization. p. 46–74. *In* B. Parthier and D. Boulter (ed.) Encyclopedia of plant physiology, New Ser., Vol. XIVb. Springer-Verlag, Berlin.

----, M.D. Bennett, J.B. Smith, and D.B. Smith. 1974. Genome size and the proportion of repeated sequence DNA in plants. Biochem. Genet. 12:257–269.

----, and R. Mathias. 1984. Genetic engineering. Prospects for transforming monocot crop plants. Nature (London) 307:108–109.

----, and M. O'Dell. 1976. Ribosomal RNA genes on homoeologous chromosomes of groups 5 and 6 in hexaploid wheat. Heredity 37:377–385.

----, ----, and J. Hutchinson. 1980. Nucleotide sequence organization in plant chromosomes and evidence for sequence translocation during evolution. Cold Spring Harb. Symp. Quant. Biol. 45:501–508.

----, ----, J. Rimpau, and D. Smith. 1978. Biochemical detection of alien DNA incorporated into wheat by chromosome engineering. Heredity 40:439–455.

----, ----, and D. Smith. 1979. Repeated sequence DNA comparisons between *Triticum* and *Aegilops* species. Heredity 42:309–322.

----, J. Rimpau, and D.B. Smith. 1977. Repeated sequence DNA relationships in four cereal genomes. Chromosoma 63:205–222.

----, and D.B. Smith. 1974a. Variation in nucleolar organizer rRNA gene multiplication in wheat and rye. Chromosoma 47:327–334.

----, and ----. 1974b. The role of homoeologous group 1 chromosomes in the control of rRNA genes in wheat. Biochem. Genet. 12:271–279.

----, and ----. 1976. Nucleotide sequence organisation in the wheat genome. Heredity 37:231–252.

Forde, J., P.R. Shewry, B.G. Forde, R.P. Fry, M. Kreis, and B.J. Miflin. 1984. The molecular biology of wheat gluten polypeptides. Second Workshop on Gluten Proteins, Wageningen, Netherlands. (Abstr.)

Francis, D., and M.D. Bennett. 1982. Replicon size and mean rate of DNA synthesis in rye (*Secale cereale* L. cv. Petkus Spring). Chromosoma 86:115–122.

Frawley, R.T., and R.B. Horsch. 1983. In vitro plant transformation systems using lysozymes and bacterial co-cultivation. p. 177–194. *In* T. Kosuge et al. (ed.) Basic life sciences. Plenum Press, New York.

Fu, T.K., and E.R. Sears. 1973. The relationship between chiasmata and crossing over in *Triticum aestivum*. Genetics 75:231–246.

Fullington, J.G., E.W. Cole, and D.D. Kasarda. 1980. Quantitative SDS-PAGE of total protein from different wheat varieties. J. Sci. Food Agric. 31:43–53.

Funaki, K., S. Matsui, and M. Sasaki. 1975. Location of nucleolar organizers in animal and

plant chromosomes by means of an improved N-banding technique. Chromosoma 49:357–370.

Gale, M.D., C.N. Law, A.J. Chojecki, and R.A. Kempton. 1983. Genetic control of α-amylase production in wheat. Theor. Appl. Genet. 64:309–316.

Galili, G., and M. Feldman. 1983a. Genetic control of endosperm proteins in wheat. 1. The use of high resolution one-dimensional gel electrophoresis for the allocation of genes coding for endosperm protein subunits in the common wheat cultivar Chinese Spring. Theor. Appl. Genet. 64:97–101.

----, and ----. 1983b. Genetic control of endosperm proteins in wheat. 2. Variation in high molecular weight glutenin and gliadin subunits of *Triticum aestivum*. Theor. Appl. Genet. 66:77–86.

García-Olmedo, F., P. Carbonero, and B.L. Jones. 1982. Chromosomal locations of genes that control wheat endosperm proteins. Adv. Cereal Sci. Technol. 5:1–47.

Gerlach, W.L. 1977. N-banded karyotypes of wheat species. Chromosoma 62:49–56.

----, R. Appels, E.S. Dennis, and W.J. Peacock. 1979. Evolution and analysis of wheat genomes using highly repeated DNA sequences. p. 81–91. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Ind. Soc. Genet. Plant Breeding, Indian Agric. Res. Inst., New Delhi.

----, and J.R. Bedbrook. 1979. Cloning and characterisation of ribosomal RNA genes from wheat and barley. Nucleic Acids Res. 7:1869–1885.

----, E.S. Dennis, and W.J. Peacock. 1983. Molecular cytogenetics of wheat. p. 191–212. *In* M.S. Swaminathan et al. (ed.) Cytogenetics of crop plants. Macmillan, New Delhi, India.

----, and T.A. Dyer. 1980. Sequence organization of the repeating units in the nucleus of wheat which contain 5S rRNA genes. Nucleic Acids Res. 8:4851–4865.

----, T.E. Miller, and R.B. Flavell. 1980. The nucleolus organizers of diploid wheats revealed by in situ hybridization. Theor. Appl. Genet. 58:97–100.

----, and W.J. Peacock. 1980. Chromosomal locations of highly repeated DNA sequences in wheat. Heredity 44:269–276.

Ghosh, H.P., K. Ghosh, M. Simsek, and U.L. RajBhandary. 1982. Nucleotide sequence of wheat germ cytoplasmic initiator methionine transfer ribonucleic acid. Nucleic Acids Res. 10:3241–3247.

Gill, B.S. 1981. Evolutionary relationships based on heterochromatin bands in six species of the *Triticinae*. J. Hered. 72:391–394.

----, P.D. Chen, and E.B. Snyder. 1984. Determination of homoeology between genomes of certain cereal species by N-banding analysis. Genetics 107:37–38.

----, and G. Kimber. 1974a. Giemsa C-banding and the evolution of wheat. Proc. Natl. Acad. Sci. USA 71:4086–4090.

----, and ----. 1974b. The Giemsa C-banded karyotype of rye. Proc. Natl. Acad. Sci. USA 71:1247–1249.

----, and ----. 1974c. A Giemsa C-banding technique for cereal chromosomes. Cereal Res. Commun. 2:87–94.

Gillies, C.J. 1981. Electron microscopy of spread maize pachytene synaptonemal complexes. Chromosoma 83:575–591.

Giráldez, R., M.C. Cermeño, and J. Orellana. 1979. Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye. Z. Pflanzenzuecht. 83:40–48.

Grabar, P., M.J. Escribano, N. Benhamou, and J. Daussant. 1965. Immunochemical study of wheat, barley, and malt proteins. J. Agric. Food Chem. 13:392–398.

Gray, M.W., L. Bonen, D. Falconet, T.Y. Huh, M.N. Schnare, and D.F. Spencer. 1982. Mitochondrial ribosomal RNAs of *Triticum aestivum* (wheat): Sequence analysis and gene organization. p. 483–488. *In* P. Slominski et al. (ed.) Mitochondrial genes. Cold Spring Harbor Laboratory Press, New York.

----, and D.F. Spencer. 1983. Wheat mitochondrial DNA encodes a eubacteria-like initiator methionine transfer RNA. FEBS Lett. 161:323–327.

Gruenbaum, Y., T. Naveh-Many, H. Cedar, and A. Razin. 1981. Sequence specificity of methylation in higher plant DNA. Nature (London) 292:860–862.

Gustafson, J.P., A.J. Lukaszewski, and M.D. Bennett. 1983. Somatic deletion and redistribution of telomeric heterochromatin in the genus *Secale* and in triticale. Chromosoma 88:293–298.

Gyarfas, J. 1978. Transference of disease resistance from *Triticum timopheevii* to *Triticum aestivum*. M.Sc. thesis. Univ. of Sydney.

Hadlaczky, G.Y., and A. Belea. 1975. C-banding in wheat evolutionary cytogenetics. Plant Sci. Lett. 4:85–88.

Hagenbuchle, O., M. Santer, J.A. Steitz, and R.J. Mans. 1978. Conservation of the primary structure of the 3′ end of 18S rRNA from eukaryotic cells. Cell 13:551–563.

Hallick, R.B., and R.B. Bottomley. 1983. Proposals for the naming of chloroplast genes. Plant Mol. Biol. Rep. 1:38–43.

Hanchinal, R.R., and J.V. Good. 1982. Seed setting and germination of AB-genome monosomic lines of PbC591 × Bijaga Yellow and their backcross generations in wheat. Wheat Inf. Serv. 55:15–21.

Hart, G.E. 1970. Evidence for triplicate genes for alcohol dehydrogenase in hexaploid wheat. Proc. Natl. Acad. Sci. USA 66:1136–1141.

———. 1973. Homoeologous gene evolution in hexaploid wheat. p. 805–810. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

———. 1975. Glutamate oxaloacetate transaminase isozymes of *Triticum*: Evidence for multiple systems of triplicate structural genes in hexaploid wheat. p. 637–657. *In* C.L. Markert (ed.) Isozymes. Vol. III. Developmental biology. Academic Press, New York.

———. 1978. Chromosomal arm locations of *Adh-R1* and an acid phosphatase structural gene in Imperial rye. Cereal Res. Commun. 6:123–133.

———. 1979a. Evidence for a triplicate set of glucosephosphate isomerase structural genes in hexaploid wheat. Biochem. Genet. 17:585–598.

———. 1979b. Genetical and chromosomal relationships among the wheats and their relatives. p. 9–29. *In* G.P. Redei (ed.) 11th Stadler Genet. Symp. Univ. Missouri Agric. Exp. Stn., Columbia, MO.

———. 1983a. Hexaploid wheat (*Triticum aestivum* L. em. Thell.). p. 35–56. *In* S.D. Tanksley and T.J. Orton (ed.) Isozymes in plant genetics and breeding, Part B. Elsevier Science Publishers B.V., Amsterdam.

———. 1983b. Discovery and genetic control of a hexaploid wheat NAD-dependent alcohol dehydrogenase which acts on aromatic alcohols. Am. J. Bot. 70(2):63. (Abstr.)

———. 1984. Biochemical loci of hexaploid wheat (*Triticum aestivum*, 2n=42, genomes AABBDD). p. 485–490. *In* S.J. O'Brien (ed.) Genetic maps. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY.

———, A.K.M.R. Islam, and K.W. Shepherd. 1980. Use of isozymes as chromosome markers in the isolation and characterization of wheat-barley chromosome addition lines. Genet. Res. 36:311–325.

———, and P.J. Langston. 1977. Chromosomal location and evolution of isozyme structural genes in hexaploid wheat. Heredity 39:263–277.

———, D.E. McMillin, and E.R. Sears. 1976. Determination of the chromosomal location of a glutamate oxaloacetate transaminase structural gene using *Triticum–Agropyron* translocations. Genetics 83:49–61.

———, and N.A. Tuleen. 1983a. Chromosomal locations of eleven *Elytrigia elongata* (= *Agropyron elongatum*) isozyme structural genes. Genet. Res. 41:181–202.

———, and ———. 1983b. Introduction and characterization of alien genetic material. p. 339–362. *In* S.D. Tanksley and T.J. Orton (ed.) Isozymes in plant genetics and breeding, Part A. Elsevier Science Publishers B.V., Amsterdam.

———, and ———. 1984. Characterizing and selecting alien genetic material in derivatives of wheat-alien species hybrids by analyses of isozyme variation. p. 377–385. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 Nov.–3 Dec. 1983. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University.

Hearn, M.T.W., F.E. Regnier, and C.T. Wehr. 1982. HPLC of peptides and proteins. Am. Lab. 14:18, 20, 23–4, 27–30, 35–6, 38–9.

Helbaek, H. 1959. Domestication of food plants in the Old World. Science 130:365–372.

Hemleben, V., and D. Grierson. 1978. Evidence that in higher plants the 25S and 18S rRNA genes are not interspersed with genes for 5S rRNA. Chromosoma 65:353–358.

Herrera-Estrella, L., G. Van den Broeck, R. Maenhaut, M. Van Montagu, J. Schell, M. Timko, and A. Cashmore. 1984. Light-inducible and chloroplast-associated expression of a chimaeric gene introduced into *Nicotiana tabacum* using a Ti plasmid vector. Nature (London) 310:115–120.

Hobolth, P. 1981. Chromosome pairing in allohexaploid wheat var. Chinese Spring. Transformation of multivalents into bivalents, a mechanism for exclusive bivalent formation. Carlsberg Res. Commun. 46:129–173.

Howe, C.J., A.D. Auffret, A. Doherty, C.M. Bowman, T.A. Dyer, and J.C. Gray. 1982a. Location and nucleotide sequence of the gene for the proton-translocating subunit of wheat chloroplast ATP synthase. Proc. Natl. Acad. Sci. USA 79:6903–6907.

----, C.M. Bowman, T.A. Dyer, and J.C. Gray. 1982b. Localization of wheat chloroplast genes for the beta and epsilon subunits of ATP synthase. Mol. Gen. Genet. 186:525–530.

----, ----, ----, and ----. 1983. The genes for the alpha and proton-translocating subunits of wheat chloroplast ATP synthase are close together on the same strand of chloroplast DNA. Mol. Gen. Genet. 190:51–55.

Hsu, T.C. 1973. Longitudinal differentiation of human chromosomes. Annu. Rev. Genet. 7:153–176.

Huebner, F.R. 1970. Comparative studies on glutenins from different classes of wheat. J. Agric. Food Chem. 18:256–259.

----, and J.A. Bietz. 1984. Separation of wheat gliadins by preparative reversed-phase high-performance liquid chromatography. Cereal Chem. 61:544–549.

Huguet, T., and L. Jouanin. 1972a. The heterogeneity of wheat nuclear DNA. Biochim. Biophys. Acta 262:431–440.

----, and ----. 1972b. Wheat DNA : Study of the heavy satellite in $Ag^{+}Cs_2SO_4$ density gradients. Biochem. Biophys. Res. Commun. 46:1169–1174.

----, ----, and S. Bazetoux. 1975. Occurrence of palindromic sequences in wheat DNA. Plant Sci. Lett. 5:379–385.

Huh, T.Y., and M.W. Gray. 1982. Conservation of ribosomal RNA gene arrangement in the mitochondrial DNA of angiosperms. Plant Mol. Biol. 1:245–249.

Hussein, K.R.F., N. Eustatiu, and H. Stegemann. 1977. Comparison between buffers, ethanol, chloroethanol, and isopropanol as extractants of wheat proteins used for separation procedures in polyacrylamide gel-electrophoresis. Rev. Roum. Biochim. 14:247–251.

----, and H. Stegemann. 1978. Comparison of proteins from wheat kernels by various electrophoretic methods in polyacrylamide. Z. Acker Pflanzenbau 146:68–78.

Hutchinson, J., V.E. Chapman, and T.E. Miller. 1980. Chromosome pairing at meiosis in hybrids between *Aegilops* and *Secale* species: A study by in situ hybridisation using cloned DNA. Heredity 45:245–254.

----, R.B. Flavell, and J. Jones. 1981. Physical mapping of plant chromosomes by in situ hybridization. p. 207–222. *In* J.K. Setlow and A. Hollaender (ed.) Genetic engineering, Vol. III. Plenum Press, New York.

----, and D.M. Lonsdale. 1982. The chromosomal distribution of cloned highly repetitive sequences from hexaploid wheat. Heredity 48:371–376.

----, and T.E. Miller. 1982. The nucleolar organisers of tetraploid and hexaploid wheats revealed by in situ hybridisation. Theor. Appl. Genet. 61:285–288.

----, ----, J. Jahier, and K.W. Shepherd. 1982. Comparison of the chromosomes of *Triticum timopheevi* with related wheats using the techniques of C-banding and *in situ* hybridization. Theor. Appl. Genet. 64:31–40.

----, ----, and S.M. Reader. 1983. C-banding at meiosis as a means of assessing chromosome affinities in the Triticeae. Can. J. Genet. Cytol. 25:319–323.

----, and A.G. Seal. 1983. A sequential in-situ hybridisation and C-banding technique. Heredity 51:507–509.

Iordansky, A.B., T.G. Zurabishvili, and N.S. Badaev. 1978. Linear differentiation of cereal chromosomes. I. Common wheat and its supposed ancestors. Theor. Appl. Genet. 51:145–152.

Irani, B.N., and C.R. Bhatia. 1972. Chromosomal location of alcohol dehydrogenase gene(s) in rye, using wheat–rye addition lines. Genetica 43:195–200.

Islam, A.K.M.R. 1980. Identification of wheat-barley addition lines with N-banding of chromosomes. Chromosoma 76:365–373.

----, K.W. Shepherd, and D.H.B. Sparrow. 1981. Isolation and characterization of euplasmic wheat–barley chromosome addition lines. Heredity 46:161–174.

Jaaska, V. 1976. Aspartate aminotransferase isoenzymes in the polyploid wheats and their diploid relatives: On the origin of tetraploid wheats. Biochem. Physiol. Pflanz. 170:159–171.

----. 1978a. Electrophoretic study of acid phosphatase isoenzymes in the grass genus *Aegilops* L. Biochem. Physiol. Pflanz. 172:133–153.

----. 1978b. NADP-dependent aromatic alcohol dehydrogenase in polyploid wheats and their diploid relatives: On the origin and phylogeny of polyploid wheats. Theor. Appl. Genet. 53:209–217.

----. 1980. Electrophoretic survey of seedling esterases in wheats in relation to their phylogeny. Theor. Appl. Genet. 56:273–284.

----. 1981. Aspartate aminotransferase and alcohol dehydrogenase isoenzymes: Intraspecific differentiation in *Aegilops tauschii* and the origin of the D genome polyploids in the wheat group. Plant Syst. Evol. 137:259–273.

----. 1983. Secale and triticale. p. 79–101. *In* S.D. Tanksley and T.J. Orton (ed.) Isozymes in genetics and plant breeding, Part B. Elsevier Science Publishers, B.V., Amsterdam.

Jackson, E.A., L.M. Holt, and P.I. Payne. 1983. Characterization of high-molecular-weight gliadin and low-molecular-weight glutenin subunits of wheat endosperm by two-dimensional electrophoresis and the chromosomal localisation of their controlling genes. Theor. Appl. Genet. 66:29–37.

Jendrisak, J. 1980. Purification, structures and functions of the nuclear RNA polymerases from higher plants. p. 77–92. *In* C.J. Leaver (ed.) Genome organization and expression in plants. Plenum Press, New York.

Jenkins, G. 1983. Chromosome pairing in *Triticum aestivum* cv. Chinese Spring. Carlsberg Res. Commun. 48:255–283.

Jewell, D.C. 1979. Chromosome banding in *Triticum aestivum* cv. Chinese Spring and *Aegilops variabilis*. Chromosoma 71:129–134.

----. 1981. Recognition of two types of positive staining material by manipulation of critical steps in the N-banding technique. Stain Technol. 56:227–234.

----, and C.J. Driscoll. 1983. The addition of *Aegilops variabilis* chromosomes to *Triticum aestivum* and their identification. Can. J. Genet. Cytol. 25:76–84.

Johnson, B.L. 1972. Seed protein profiles and the origin of the hexaploid wheats. Am. J. Bot. 59:952–960.

----. 1975. Identification of the apparent B-genome donor of wheat. Can. J. Genet. Cytol. 17:21–39.

----, and O. Hall. 1965. Analysis of phylogenetic affinities in the *Triticinae* by protein electrophoresis. Am. J. Bot. 52:506–513.

Johnson, V.A., P.J Mattern, and J.W. Schmidt. 1972. Genetic studies of wheat proteins. p. 126–135. *In* G.E. Inglett (ed.) Symposium on seed proteins. AVI Publishing Co., Westport, CT.

Jones, J.D.G. 1981. Repeated DNA sequences in rye (*Secale cereale*), wheat (*Triticum aestivum*) and their relatives. Ph.D. thesis. Univ. Cambridge, Cambridge.

----, and R.B. Flavell. 1982a. The mapping of highly-repeated DNA families and their relationship to C-bands in chromosomes of *Secale cereale*. Chromosoma 86:595–612.

----, and ----. 1982b. The structure, amount and chromosomal localisation of defined repeated DNA sequences in species of the genus *Secale*. Chromosoma 86:613–641.

Jones, R.W., N.W. Taylor, and F.R. Senti. 1959. Electrophoresis and fractionation of wheat gluten. Arch. Biochem. Biophys. 84:363–376.

Joppa, L.R. 1973. Development of D-genome disomic substitution lines of durum wheat (*Triticum turgidum* L.). p. 685–690. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

----, K. Khan, C. Josephides, and N.D. Williams. 1983a. Chromosomal location of genes affecting quality in durum wheat. p. 297–301. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University.

----, ----, and N.D. Williams. 1983b. Chromosomal location of genes for gliadin polypeptides in durum wheat (*Triticum turgidum* L.). Theor. Appl. Genet. 64:289–293.

----, and S.S. Maan. 1982. A durum wheat disomic-substitution line having a pair of chromosomes from *Triticum boeoticum*: Effect on germination and growth. Can. J. Genet. Cytol. 24:549–557.

----, and N.D. Williams. 1977. D-genome substitution-monosomics of durum wheat. Crop Sci. 17:772–776.

----, and N.D. Williams. 1979. A disomic-5D-nullisomic-5B substitution line of durum wheat. Crop Sci. 19:509–511.

----, and ----. 1983. The Langdon durum D-genome disomic substitutions: Development, characteristics, and uses. Agron. Abstr. American Society of Agronomy, Madison, WI. p. 68.

Joudrier, P., and Y. Cauderon. 1976. Localisation chromosomique de genes controlant de certains constituants β-amylasique du grain de blé tendre. C. R. Hebd. Seances Acad. Sci. Ser. D. 282:115–118.

Kahler, A.L., and R.W. Allard. 1970. Genetics of isozyme variants in barley. I. Esterases. Crop Sci. 10:444–448.

Kasarda, D.D., J.-C. Autran, E. J.-L. Lew, C.C. Nimmo, and P.R. Shewry. 1983. N-terminal amino acid sequences of ω-gliadins and ω-secalins. Implications for the evolution of prolamin genes. Biochim. Biophys. Acta 747:138–150.

----, J.E. Bernardin, and C.C. Nimmo. 1976. Wheat proteins. Adv. Cereal Sci. 1:158–236.

----, D.A. Da Roza, and J.I. Ohms. 1974. N-terminal sequence of α_2-gliadin. Biochim. Biophys. Acta 351:290–294.

----, D. Lafiandra, R. Morris, and P.R. Shewry. 1984a. Genetic relationships of wheat gliadin proteins. *In* Proc. 3rd Symp. Seed Proteins (Gatersleben, G.D.R.) Kulturpflanze (Berlin) 32:41–61.

----, T.W. Okita, J.E. Bernardin, P.A. Baecker, C.C. Nimmo, E.J.-L. Lew, M.D. Dietler, and F.C. Greene. 1984b. Nucleic acid (cDNA) and amino acid sequences of α-type gliadins from wheat (*Triticum aestivum*). Proc. Natl. Acad. Sci. USA 81:4712–4716.

Kerber, E.R. 1964. Wheat: Reconstitution of the tetraploid component (AABB) of hexaploids. Science 143:253–255.

Kersten, W., H. Kersten, and W. Szybalski. 1966. Physicochemical properties of complexes between DNA and antibiotics which affect RNA synthesis (actinomycin, daunomycin, cinerubin, nogalomycin, chromomycin, mithramycin, olivomycin). Biochem. 5:236–244.

Khan, K. 1982. Polyacrylamide gel electrophoresis of wheat gluten proteins. Baker's Dig. 56(5):14–19.

----, C.E. McDonald, and O.J. Banasik. 1983. Polyacrylamide gel electrophoresis of gliadin proteins for wheat variety identification—Procedural modifications and observations. Cereal Chem. 60:178–181.

Kihara, H. 1919. Über cytologische Studien bei einige Getreidearten. I. Species-Bastarde des Weizens und Weizenroggen-Bastarde. Bot. Mag. Tokyo 32:17–38.

----. 1924. Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem. Coll. Sci., Kyoto Imp. Univ., B:1–200.

----. 1944. Discovery of the DD-analyser, one of the ancestors of *vulgare* wheats. Agric. Hort. (Tokyo) 19:889–890.

Kimber, G. 1971. The rationale of measuring chromosomes. Seiken Zihô 22:5–8.

----. 1982. The genomic relationships of *Triticum tripsacoides*. Z. Pflanzenzuecht. 89:289–294.

----. 1983. The suppression of characters of generic importance in hybrids and amphiploids in the *Triticeae*. Cereal Res. Commun. 11:9–14.

----, and L.C. Alonso. 1981. The analysis of meiosis in hybrids. III. Tetraploid hybrids. Can. J. Genet. Cytol. 23:235–254.

----, ----, and P.J. Sallee. 1981. The analysis of meiosis in hybrids. I. Aneuploid hybrids. Can. J. Genet. Cytol. 23:209–219.

----, and R.S. Athwal. 1972. A reassessment of the course of evolution of wheat. Proc. Natl. Acad. Sci. USA 69:912–915.

----, and M. Abu Bakar. 1981. The genomic relationships of *Triticum dichasians* and *T. umbellulatum*. Z. Pflanzenzuecht 87:265–273.

----, D. Pignone, and P.J. Sallee. 1983. The relationships of the M and M^u genomes of *Triticum*. Can. J. Genet. Cytol. 25:509–512.

----, and E.R. Sears. 1970. Nomenclature for the description of aneuploids in the *Triticinae*. Annu. Wheat Newsl. 16:14–19.

----, and ----. 1983. Assignment of genome symbols in the *Triticeae*. p. 1195–1196. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University.

----, and Y.H. Zhao. 1983. The D genome of the *Triticeae*. Can. J. Genet. Cytol. 25:581–589.

----, and ----. 1984. The D genome of *Triticum cylindricum*. Cereal Res. Commun. 12:255–257.

Kling, H. 1975. Immunochemische Untersuchungen an Prolaminen. Z. Pflanzenphysiol. 76:155–162.

Kobrehel, K. 1978. Identification of chromosome segments controlling the synthesis of peroxidases in wheat seeds and in transfer lines with *Agropyron elongatum*. Can. J. Bot. 56:1091–1094.

----, and P. Feillet. 1975. Identification of genomes and chromosomes involved in peroxidase synthesis of wheat seeds. Can. J. Bot. 53:2336–2344.

Koebner, R.M.D., and K.W. Shepherd. 1983. Shikimate dehydrogenase—a biochemical marker for group 5 chromosomes in the *Triticinae*. Genet. Res. 41:209–213.

Koller, B., H. Delius, and T.A. Dyer. 1982. The organisation of the chloroplast DNA in wheat and maize in the region containing the LS gene. Eur. J. Biochem. 122:17–23.

Koller, O.L., and F.J. Zeller. 1976. The homoeologous relationships of rye chromosomes 4R and 7R with wheat chromosomes. Genet. Res. 28:177–188.

Kolodner, R., and K.K. Tewari. 1975. The molecular size and conformation of the chloroplast DNA from higher plants. Biochim. Biophys. Acta 402:372–390.

Konarev, A.V. 1981. The genome specific grain proteins and the phylogenetic interrelation between *Triticum* L., *Elytrigia* Desf., *Elymus* L. and *Agropyron* Gaertn. Theor. Appl. Genet. 59:117–121.

Konarev, V.G., I.P. Gavrilyuk, N.K. Gubareva, and T.I. Peneva. 1979. Seed proteins in genome analysis, cultivar identification, and documentation of cereal genetic resources: A review. Cereal Chem. 56:272–278.

Kosmolak, F.G., J.E. Dexter, R.R. Matsuo, D. Leisle, and B.A. Marchylo. 1980. A relationship between durum wheat quality and gliadin electrophoregrams. Can. J. Plant Sci. 60:427–432.

Kozak, M. 1981. Possible role of flanking nucleotides in recognition of the AUG initiator codon by eukaryotic ribosomes. Nucleic Acids Res. 9:5233–5252.

Kuspira, J., and L.A. Millis. 1967. Cytogenetic analysis of tetraploid wheats using hexaploid aneuploids. Can. J. Genet. Cytol. 9:79–86.

Laird, C.D., B.L. McConaughy, and B.J. McCarthy. 1969. On the rate of fixation of nucleotide substitutions in evolution. Nature (London) 224:149–154.

Langston, P.J., G.E. Hart, and C.N. Pace. 1979. Purification and characterization of alcohol dehydrogenase from wheat. Arch. Biochem. Biophys. 196:611–618.

----, C.N. Pace, and G.E. Hart. 1980. Wheat alcohol dehydrogenase isozymes. Purification, characterization, and gene expression. Plant Physiol. 65:518–522.

Laroche, A., J. Plante, B. Beaumont, and G.G. Poirier. 1980. ADP-ribosylation of rye histones. Can. J. Biochem. 58:692–695.

Larsen, J., and G. Kimber. 1973. Chromosome length and arm ratio of *Triticum turgidum* and *T. tauschii* studied by a new method. p. 691–696. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Law, C.N., and A.J. Worland. 1973. Aneuploidy in wheat and its uses in genetic analysis. p. 25–65. *In* H.W. Howard et al. (ed.) Annu. Rep. 1972, Plant Breeding Institute, Cambridge.

Lawrence, G.J., and K.W. Shepherd. 1980. Variation in glutenin protein subunits of wheat. Aust. J. Biol. Sci. 33:221–233.

----, and ----. 1981a. Chromosomal location of genes controlling seed proteins in species related to wheat. Theor. Appl. Genet. 59:25–31.

----, and ----. 1981b. Inheritance of glutenin protein subunits of wheat. Theor. Appl. Genet. 60:333–337.

Leaver, C.J., and M.W. Gray. 1982. Mitochondrial genome organization and expression in higher plants. Annu. Rev. Plant Physiol. 33:373–402.

Li, J., and Y.-N. Liu. 1983. Chloroplast DNA and cytoplasmic male-sterility. Theor. Appl. Genet. 64:231–238.

Liang, G.H., A.S. Wang, and R.L. Phillips. 1978. Control of ribosomal RNA gene multiplicity in wheat. Can. J. Genet. Cytol. 19:425–435.

Lilienfeld, F.A. 1951. H. Kihara: Genome-analysis in *Triticum* and *Aegilops*. Concluding review. Cytologia 16:101–123.

Linde-Laursen, I. 1975. Giemsa C-banding of the chromosomes of 'Emir' barley. Hereditas 81:285–289.

Loegering, W.Q., and E.R. Sears. 1970. *Sr9d*, a gene in Hope wheat for reaction to *Puccinia graminis tritici*. Z. Pflanzenzuecht. 64:335–339.

Longwell, J.H., Jr., and E.R. Sears. 1963. Nullisomics in tetraploid wheat. Am. Nat. 97:401–403.

Lonsdale, D.M., T.P. Hodge, C.J. Howe, and D.B. Stern. 1983. Maize mitochondrial DNA contains a sequence homologous to the ribulose-1,5-bisphosphate carboxylase large subunit gene of chloroplast DNA. Cell 34:1007–1014.

Lookhart, G.L., B.L. Jones, S.B. Hall, and K.F. Finney. 1982. An improved method for standardizing polyacrylamide gel electrophoresis of wheat gliadin proteins. Cereal Chem. 59:178–181.

Lukaszewski, A.J., and J.P. Gustafson. 1983. Translocations and modifications of chromosomes in triticale × wheat hybrids. Theor. Appl. Genet. 64:239–248.

Maan, S.S. 1973. Cytoplasmic variability in the *Triticinae*. p. 367–373. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

----. 1977. Fertility of amphihaploids in *Triticinae*. J. Hered. 68:87–94.

MacIntyre, R.J. 1976. Evolution and ecological value of duplicate genes. Annu. Rev.Ecol. Syst. 7:421–468.

Mackay, R.M., D.F. Spencer, W.F. Doolittle, and M.W. Gray. 1980. Nucleotide sequences of wheat-embryo cytosol 5-S and 5.8-S ribosomal ribonucleic acids. Eur. J. Biochem. 112:561–576.

Maier, G., and K. Wagner. 1980. Routinemethode zur Identifizierung von Weizensorten mit Hilfe der Polyacrylamidgelelektrophorese. Z. Lebensm. Unters. Forsch. 170:343–345.

Martini, G., and A. Bozzini. 1967. Ottenimento di aneuploidi mediante irraggiamento di gameti in frumento duro. Genet. Agrar. 21:139–147.

May, C.E. 1983. Triticale × wheat hybrids and the introduction of speckled leaf blotch resistance to wheat. p. 175–179. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant. Germ-Plasm Institute, Fac. Agric., Kyoto University.

----, and R. Appels. 1980. Rye chromosome translocations in hexaploid wheat: A re-evaluation of the loss of heterochromatin from rye chromosomes. Theor. Appl. Genet. 56:17–23.

----, and ----. 1982. The inheritance of rye chromosomes in early generations of triticale × wheat hybrids. Can. J. Genet. Cytol. 24:285–291.

----, and ----. 1984. Seedling lethality in wheat: A novel phenotype associated with a 2RS/2BL translocation chromosome. Theor. Appl. Genet. 68:163–168.

----, R.S. Vickery, and C.J. Driscoll. 1973. Gene control in hexaploid wheat. p. 843–849. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

McCausland, J., and C.W. Wrigley. 1976. Electrophoretic analysis of wheat and rye mixtures in meal, flour, and baked goods. J. Sci. Food Agric. 27:1197–1202.

McFadden, E.S., and E.R. Sears. 1944. The artificial synthesis of *Triticum spelta*. Rec. Genet. Soc.Am. 13:26–27. (Abstr.)

----, and ----. 1946. The origin of *Triticum spelta* and its free-threshing hexaploid relatives. J. Hered. 37.81–89, 107–116.

McIntosh, R.A. 1972. Cytogenetical studies in wheat VI. Chromosome location and linkage studies involving *Sr13* and *Sr8* for reaction to *Puccinia graminis* f. sp. *tritici*. Aust. J. Biol. Sci. 25:765–773.

----. 1973. A catalogue of gene symbols for wheat, 1973. p. 893–938. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

----. 1980. Chromosome location and linkage studies involving the wheat stem rust resistance gene *Sr14*. Cereal Res. Commun. 8:315–320.

----. 1983. A catalogue of gene symbols for wheat (1983 edition). p. 1197–1254. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University.

----, and E.P. Baker. 1968a. Cytogenetical studies in wheat. II. An analysis of chlorophyll abnormalities in hexaploid wheat. Genet. Res. 12:11–19.

----, and E.P. Baker. 1968b. A linkage map for chromosome 2D. p. 305–309. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Canberra, Australia. 5–9 August. Australian Academy of Science, Canberra.

----, and N.H. Luig. 1973. Recombination between genes for reaction to *P. graminis* at or near the *Sr9* locus. p. 425–432. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

----, ----, and E.P. Baker. 1967. Genetic and cytogenetic studies of stem rust, leaf rust and powdery mildew resistances in Hope and related wheat cultivars. Aust. J. Biol. Sci. 20:1181–1192.

Mecham, D.K., D.D. Kasarda, and C.O. Qualset. 1978. Genetic aspects of wheat gliadin proteins. Biochem. Genet. 16:831–853.

Mello-Sampayo, T. 1968. Homoeologous chromosome pairing in pentaploid hybrids of wheat. p. 179–184. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Canberra, Australia. 5–9 August. Australian Academy of Science, Canberra.

----. 1971. Genetic regulation of meiotic chromosome pairing by chromosome 3D of *Triticum aestivum*, Nature New Biol. 230:22–23.

----. 1972. Compensated monosomic 5B-trisomic 5A plants in tetraploid wheat. Can. J. Genet. Cytol. 14:463–475.

----, and A.P. Canas. 1973. Suppressors of meiotic chromosome pairing in common wheat.

p. 709–713. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Merker, A. 1973. A Giemsa technique for rapid identification of chromosomes in triticale. Hereditas 75:280–282.

Messing, J., D. Geraghty, G. Heidecker, N.T. Hu, J. Kridl, and I. Rubenstein. 1983. Plant gene structure. p. 211–227. *In* T. Kosuge et al., (ed.) Genetic engineering of plants: An agricultural perspective. Plenum Press, New York.

Miflin, B.J., and P.R. Shewry. 1979. The biology and biochemistry of cereal seed proteins. p. 137–158. *In* Seed protein improvement in cereals and grain legumes. Vol. I. IAEA, Vienna.

Miller, T.E., W.L. Gerlach, and R.B. Flavell. 1980. Nucleolus organiser variation in wheat and rye revealed by in situ hybridisation. Heredity 44:377–382.

----, J. Hutchinson, and V. Chapman. 1982a. Investigation of a preferentially transmitted *Aegilops sharonensis* chromosome in wheat. Theor. Appl. Genet. 61:27–33.

----, ----, and S.M. Reader. 1983. The identification of the nucleolus organiser chromosomes of diploid wheat. Theor. Appl. Genet. 65:145–147.

----, S.M. Reader, and V. Chapman. 1982b. The addition of *Hordeum chilense* chromosomes to wheat. p. 79–81. *In* Induced variability in plant breeding. EUCARPIA, Int. Symp., Wageningen, Netherlands. 31 August–4 September. PUDOC, Wageningen.

----, K.W. Shepherd, and R. Riley. 1981. The relationship of chromosome 4A of diploid wheat to that of hexaploid wheat: A clarification of an earlier study. Cereal Res. Commun. 9:327–329.

Mitra, R., and C.R. Bhatia. 1973. Repeated and non-repeated nucleotide sequences in diploid and polyploid wheat species. Heredity 31:251–262.

Mochizuki, A. 1968. The monosomics of durum wheat. p. 310–315. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Canberra, Australia. 5–9 August. Australian Academy of Science, Canberra.

----. 1970. Production of three monosomic series in emmer and common wheat. Seiken Zihô 22:39–49.

Moonen, J.H.E., A. Scheepstra, and A. Graveland. 1982. Use of the SDS-sedimentation test and SDS-polyacrylamidegel electrophoresis for screening breeder's samples for bread-making quality. Euphytica 31:677–690.

Morris, R., J.W. Schmidt, P.J. Mattern, and V.A. Johnson. 1966. Chromosomal location of genes for flour quality in the wheat variety 'Cheyenne' using substitution lines. Crop Sci. 6:119–122.

----, and E.R. Sears. 1967. The cytogenetics of wheat and its relatives. p. 19–87. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy:13.

Mubumbila, M., C.M. Bowman, F. Droog, T. Dyer, M. Kuntz, and J.H. Weil. 1985. Chloroplast transfer RNAs and tRNA genes of wheat. Plant Mol. Biol. 4:315–322.

Muthukrishnan, S., B.S. Gill, M. Swegle, and G. Ram Chandra. 1985. Structural genes for α-amylases are located in barley chromosomes 1 and 6. J. Biol. Chem. 259:13637–13639.

Nakai, Y. 1979a. Isozyme variations in *Aegilops* and *Triticum*, IV. The origin of the common wheats revealed from the study on esterase isozymes in synthesized hexaploid wheats. Jpn. J. Genet. 54:175–189.

----. 1979b. The origin of the tetraploid wheats revealed from the study on esterase isozymes. p. 108–119. *In* S. Ramanujam (ed.) Proc. 5th Int.Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Ind. Soc. Genet. Plant Breeding, Ind. Agric. Res. Inst., New Delhi.

----. 1981. D genome donors for *Aegilops cylindrica* (CCDD) and *Triticum aestivum* (AABBDD) deduced from esterase isozyme analysis. Theor. App. Genet. 60:11–16.

----. 1982. D genome donors for *Aegilops crassa* ($DDM^{cr}M^{cr}$, $DDD^2D^2M^{cr}M^{cr}$) and *Aegilops vavilovii* ($DDM^{cr}M^{cr}S^pS^p$) deduced from esterase analysis by isoelectric focusing. Jpn. J. Genet. 57:349–360.

Natarajan, A.T., and N.P. Sarma. 1974. Chromosome banding patterns and the origin of the B genome in wheat. Genet. Res. 24:103–108.

Nath, J., J.J. Hanzel, J.P. Thompson, and J.W. McNay. 1984. Additional evidence implicating *Triticum searsii* as the B-genome donor to wheat. Biochem. Genet. 22:37–50.

----, J.W. McNay, C.M. Paroda, and S.C. Gulati. 1983. Implication of *Triticum searsii* as the B-genome donor to wheat using DNA hybridizations. Biochem. Genet. 21:745–760.

Neuman, P.R., and G.E. Hart. 1983. Genetic control of shikimate dehydrogenase in hexaploid wheat. Biochem. Genet. 21:963–968.

----, and ----. 1986. Genetic control of the mitochondrial form of superoxide dismutase in hexaploid wheat. Biochem. Genet. 24:435–446.

Nishikawa, K. 1971. Telosomic lines of tetraploid wheat. Eur. Wheat Aneuploid Co-operative Newsl. 3:65–66.

----, and Y. Furuta. 1979. DNA content of nucleus and individual chromosomes and its evolutionary significance. p. 133–138. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Ind. Soc. Genet. Plant Breeding, Ind. Agric. Res. Inst., New Delhi.

----,----, Y. Hina, and T. Yamada. 1981. Genetic studies of α-amylase isozymes in wheat. IV. Genetic analyses in hexaploid wheat. Jpn. J. Genet. 56:385–395.

----, ----, and T. Wada. 1980. Genetic studies on α-amylase isozymes in wheat. III. Intraspecific variation in *Aegilops squarrosa* and birthplace of hexaploid wheat. Jpn. J. Genet. 55:325–336.

----, and M. Nobuhara. 1971. Genetic studies of α-amylase isozymes in wheat. I. Location of genes and variation in tetra- and hexaploid wheat. Jpn. J. Genet. 46:345–353.

Noda, K., and K.J. Kasha. 1978. A proposed barley karyotype revision based on C-band chromosome identification. Crop Sci. 18:925–931.

Noronha-Wagner, M., and T. Mello-Sampayo. 1966. Aneuploids in durum wheat. p. 395–408. *In* J. Mac Key (ed.) Proc. 2nd Int. Wheat Genet. Symp., Lund, Sweden. 18–24 August. Hereditas (Suppl.) Vol. 2.

Ogihara, Y., and K. Tsunewaki. 1982. Molecular basis of the genetic diversity of the cytoplasm in *Triticum* and *Aegilops*. I. Diversity of the chloroplast genome and its lineage revealed by the restriction pattern of ct-DNAs. Jpn. J. Genet. 57:371–396.

----, and ----. 1984. The diversity of chloroplast DNA among *Triticum* and *Aegilops* species. p. 407–413. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 Nov.–3 Dec. 1983. Plant Germ-Plasm Institute, Fac. Agric. Kyoto University.

Ohms, J.-P. 1980a. Elektrophoretische Sortendiagnose von Getreide. Erkennung von Weizensorten mit A-Backqualität am Verteilungsmuster der reduzierten Albumin/Globulin-Fraktion. Z. Lebensm. Unters. Forsch. 170:27–30.

----. 1980b. Möglichkeiten der Sortenkontrolle an Einzelpflanzen in Getreidesaatgutvermehrungsbeständen durch die Elektrophorese der Kornproteine. Landwirtsch. Forsch. Sonderh. 37:287–294.

Okamoto, M. 1957. Asynaptic effect of chromosome V. Wheat Inf. Serv. 5:6.

----. 1962. Identification of the chromosomes of common wheat belonging to the A and B genomes. Can. J. Genet. Cytol. 4:31–37.

----, and N. Inomata. 1974. Possibility of 5B-like effect in diploid species. Wheat Inf. Serv. 38:15–16.

Orth, R.A., and W. Bushuk. 1974. Studies of glutenin. VI. Chromosomal location of genes coding for subunits of glutenin of common wheat. Cereal Chem. 51:118–126.

Osborne, T.B. 1907. The proteins of the wheat kernel. Carnegie Institute of Washington, Washington, DC.

Palmer, J.D., and C.R. Shields. 1984. Tripartite structure of the *Brassica campestris* mitochondrial genome. Nature (London) 307:437–440.

Paris Conference. 1971. Standardization in human cytogenetics (1972). Birth defects: Original Art. Ser. VIII 7. National Foundation March of Dimes, New York.

Payne, P.I., K.G. Corfield, and J.A. Blackman. 1979. Identification of a high-molecular-weight subunit of glutenin whose presence correlates with bread-making quality in wheats of related pedigree. Theor. Appl. Genet. 55:153–159.

----, ----, L.M. Holt, and J.A. Blackman. 1981a. Correlations between the inheritance of certain high-molecular-weight subunits of glutenin and bread-making quality in progenies of six crosses of bread wheat. J. Sci. Food Agric. 32:51–60.

----, L.M. Holt, J. Hutchinson, and M.D. Bennett. 1984a. Development and characterisation of a line of bread wheat, *Triticum aestivum*, which lacks the short-arm satellite of chromosome 1B and the *Gli-B1* locus. Theor. Appl. Genet. 68:327–334.

----, ----, E.A. Jackson, and C.N. Law. 1984b. Wheat storage proteins: Their genetics and their potential for manipulation by plant breeding. Philos. Trans. R.Soc. Lond. Ser. B 304:359–371.

----, ----, and C.N. Law. 1981b. Structural and genetical studies on the high-molecular-weight subunits of wheat glutenin. Part 1. Allelic variation in subunits amongst varieties of wheat (*Triticum aestivum*). Theor. Appl. Genet. 60:229–236.

----, ----, A.J. Worland, and C.N. Law. 1982. Structural and genetical studies on the high-molecular-weight subunits of wheat glutenin. 3. Telocentric mapping of the subunit genes on the long arms of the homoeologous group 1 chromosomes. Theor. Appl. Genet. 63:129–138.

----, E.A. Jackson, and L.M. Holt. 1984c. The association between γ-gliadin 45 and gluten strength in durum wheat varieties: A direct causal effect or the result of genetic linkage? J. Cereal Sci. 2:73–81.

----, C.N. Law, and E.E. Mudd. 1980. Control by homoeologous group 1 chromosomes of the high-molecular-weight subunits of glutenin, a major protein of wheat endosperm. Theor. Appl. Genet. 58:113–120.

Peacock, W.J., W.L. Gerlach, and E.S. Dennis. 1981. Molecular aspects of wheat evolution: Repeated DNA sequences. p. 41–60. *In* L.T. Evans and W.J. Peacock (ed.) Wheat science—today and tomorrow. Cambridge University Press, Cambridge.

Person, C. 1956. Some aspects of monosomic wheat breeding. Can. J. Bot. 34:60–70.

Piazzi, S.E., G. Riparbelli, S. Sordi, P. Cantagalli, F. Pocchiari, and V. Silano. 1972. Immunochemical characterization of specific albumins of bread wheat. Cereal Chem. 49:72–78.

Pietro, M., and G.E. Hart. 1985. The genetic control of triosephosphate isomerase of hexaploid wheat and other Triticeae species. Genet. Res. 45:127–142.

Pogna, N.E., G. Boggini, M. Corbellini, M. Cattaneo, and A. Dal Belin Peruffo. 1982. Association between gliadin electrophoretic bands and quality in common wheat. Can. J. Plant Sci. 62:913–918.

Popineau, Y., and B. Godon. 1978. Application de la chromatographie d'interaction hydrophobe au fractionnement des prolamines du blé tendre. C.R. Hebd. Seances Acad. Sci. Ser. D. 287:1051–1054.

Porceddu, E., D. Lafiandra, and G.T. Scarascia-Mugnozza. 1983. Genetics of seed proteins in wheat. p. 77–141. *In* W. Gottschalk and H.P. Müller (ed.) Seed proteins—Biochemistry, genetics, nutritional value. M. Nijhoff, The Hague, Netherlands.

Powling, A., A.K.M.R. Islam, and K.W. Shepherd. 1981. Isozymes in wheat–barley hybrid derivative lines. Biochem. Genet. 19:237–254.

Preston, K.R., W. Woodbury, R.A. Orth, and W. Bushuk. 1975. Comparison of gliadin and glutenin subunits in the *Triticinae* by SDS-polyacrylamide gel electrophoresis. Can. J. Plant Sci. 55:667–672.

Quetier, F., and F. Vedel. 1980. Heterogeneous population of mitochondrial DNA molecules in higher plants. Nature (London) 268:365–368.

Rafalski, J.A., K. Scheets, M. Metzler, D.M. Peterson, C. Hedgcoth, and D.G. Söll. 1984. Developmentally regulated plant genes: The nucleotide sequence of a wheat gliadin genomic clone. EMBO J. 3:1409–1415.

Ranjekar, P.K., D. Pallotta, and J.G. Lafontaine. 1976. Characterisation of repetitive DNA in barley and wheat. Biochim. Biophys. Acta 425:30–40.

----, ----, and ----. 1978. Analysis of plant genomes. III.Denaturation and reassociation properties of cryptic satellite DNAs in barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*). Biochim. Biophys. Acta 520:103–110.

Rao, A.R. 1976. Phylogenetic relationships among *Triticum* and *Aegilops* species. Pak. J. Agric. Sci. 13:139–146.

Rees, H., and M.R. Walters. 1965. Nuclear DNA and the evolution of wheat. Heredity 20:73–82.

Regnier, F.E., and K.M. Gooding. 1980. High-performance liquid chromatography of proteins. Anal. Biochem. 103:1–25.

Richmond, T.J., J.T. Finch, B. Rushton, D. Rhodes, and A. Klug. 1984. Structure of the nucleosome core particles at 7Å resolution. Nature (London) 311:532–537.

Riley, R., and V. Chapman. 1958. Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature (London) 182:713–715.

----, and ----. 1964. Cytological determination of the homoeology of chromosomes of *Triticum aestivum*. Nature (London) 203:156–158.

----, and ----. 1967. Effect of 5BS in suppressing the expression of altered dosage of 5BL on meiotic chromosome pairing in *Triticum aestivum*. Nature (London) 216:60–62.

----, ----, R.M. Young, and A.M. Belfield. 1966. Control of meiotic chromosome pairing by the chromosomes of homoeologous group 5 of *Triticum aestivum*. Nature (London) 212:1475–1477.

Rimpau, J., D.B. Smith, and R.B. Flavell. 1978. Sequence organisation analysis of the wheat and rye genomes by interspecies DNA/DNA hybridisation. J. Mol. Biol. 123:327–359.

Rodrigues, J. de A., W.F. Brandt, and C.V. Holt. 1979. Plant histone 2 from wheat germ, a family of histone H2A variants. Biochim. Biophys. Acta 578:196–206.

Rosenberg, O. 1909. Cytologische und morphologische Studien an *Drosera longifolia* × *rotundifolia*. Kungl. Sv. Vetensk. Acad. Handl. 43:1–64.

Rothstein, S.J., C.M. Lazarus, W.E. Smith, D.C. Baulcombe, and A.A. Gatenby. 1984. Secretion of a wheat α-amylase expressed in yeast. Nature (London) 308:662–665.

Rowley, J.D. 1974. Identification of human chromosomes. p. 17–46. *In* J.J. Yunis (ed.) Human chromosome methodology. Academic Press, New York.

Rybalka, A.I., and A.A. Sozinov. 1979. Mapping the locus *Gld 1B*, which controls the biosynthesis of reserve proteins in soft wheat. Cytol. Genet. 13:276–282.

Sakamura, T. 1918. Kurze Mitteilung über die Chromosomenzahlen und die Verwandtschaftsverhältnisse der *Triticum*-Arten. Bot. Mag. 32:151–154.

Salinas, J., and C. Benito. 1985a. Chromosomal location of malate dehydrogenase structural genes in rye (*Secale cereale* L.). Z. Pflanzenzuecht. 94:208–217.

----, and ----. 1985b. Chromosomal locations of phosphoglucomutase, phosphoglucose isomerase, and glutamate oxaloacetate transaminase structural genes in different rye cultivars. Can. J. Genet. Cytol. 27:105–113.

Sarkar, P., and G.L. Stebbins. 1956. Morphological evidence concerning the origin of the B genome of wheat. Am. J. Bot. 43:297–304.

Sarma, N.P., and A.T. Natarajan. 1973. Identification of heterochromatic regions in the chromosomes of rye. Hereditas 74:233–237.

Sasaki, K., and M. Sugita. 1982. Relationship between poly (adenosine 5′-diphosphate-ribose) synthesis and transcriptional activity in wheat embryo chromatin. Plant Physiol. 69:543–545.

Sax, K. 1922. Sterility in wheat hybrids. II. Chromosome behavior in partially sterile hybrids. Genetics 7:513–552.

Schlegel, R., and B.S. Gill. 1984. N-banding analysis of rye chromosomes and the relationship between N-banded and C-banded heterochromatin. Can. J. Genet. Cytol. 22:765–769.

----, and D. Mettin. 1978. Bemerkungen zur Karyotypanalyse beim Saatweizen (*Triticum aestivum* L.). Arch. Zuechtungsforsch. 8:333–344.

----, and E. Weryszko. 1979. Intergeneric chromosome pairing in different wheat–rye hybrids revealed by the Giemsa banding technique and some implications on karyotype evolution in the genus *Secale* (In German.) Biol. zb. Lviv. Derzh. Univ. 98:399–407.

Scott, K.F., J.E. Hughes, P.M. Gresshoff, J.E. Beringer, B.G. Rolfe, and J. Shine. 1982.

Molecular cloning of *Rhizobium trifolii* genes involved in symbiotic nitrogen fixation. J. Mol. Appl. Genet. 1:315–326.

Seal, A.G. 1982. C-banded wheat chromosomes in wheat and triticale. Theor. Appl. Genet. 63:39–47.

----, and M.D. Bennett. 1981. The rye genome in winter hexaploid triticales. Can. J. Genet. Cytol. 23:647–653.

----, and ----. 1982. Preferential C-banding of wheat or rye chromosomes. Theor. Appl. Genet. 63:227–233.

Sears, E.R. 1952. Misdivision of univalents in common wheat. Chromosoma 4:535–550.

----. 1953. Nullisomic analysis in common wheat. Am. Nat. 87:245–252.

----. 1954. The aneuploids of common wheat. Missouri Agric. Exp. Stn. Res. Bull. 572.

----. 1962. The use of telocentric chromosomes in linkage mapping. Genetics 47:983. (Abstr.)

----. 1966a. Chromosome mapping with the aid of telocentrics. p. 370–381. *In* J. Mac Key (ed.) Proc. 2nd Int. Wheat Genetics Symp., Lund, Sweden. 19–24 Aug. 1963. Hereditas 2: (Suppl.)

----. 1966b. Nullisomic-tetrasomic combinations in hexaploid wheat. p. 29–45. *In* R. Riley and K.R. Lewis (ed.) Chromosome manipulations and plant genetics. Oliver and Boyd, London.

----. 1976. Genetic control of chromosome pairing in wheat. Annu. Rev. Genet. 10:31–51.

----. 1977. An induced mutant with homoeologous pairing in common wheat. Can. J. Genet. Cytol. 19:585–593.

----, W.Q. Loegering, and H.A. Rodenhiser. 1957. Identification of chromosomes carrying genes for stem rust resistance in four varieties of wheat. Agron. J. 49:208–212.

----, and M. Okamoto. 1956. Genetic and structural relationships of non-homologous chromosomes in wheat. p. 332–335. *In* Proc. Int. Genet. Symp., Tokyo. Cytologia Suppl.

----, and L.M.S. Sears. 1979. The telocentric chromosomes of common wheat. p. 389–407. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Ind. Soc. Genet. Plant Breeding, Ind. Agric. Res. Inst., New Delhi.

Shands, H., and G. Kimber. 1973. Reallocation of the genomes of *Triticum timopheevii* Zhuk. p. 101–108. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 Aug. 1973. Univ. of Missouri, Columbia.

Shchapova, A.I. 1974. Differential staining of plant chromosomes. Tsitologia 16:370–372.

Shepherd, K.W. 1968. Chromosomal control of endosperm proteins in wheat and rye. p. 86–96. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Canberra. 5–9 August. Australian Academy of Sciences, Canberra.

----, and A.C. Jennings. 1971. Genetic control of rye endosperm proteins. Experientia 27:98–99.

Shewry, P.R., J.-C. Autran, C.C. Nimmo, E.J.-L. Lew, and D.D. Kasarda. 1980. N-terminal amino acid sequence homology of storage protein components from barley and a diploid wheat. Nature (London) 286:520–522.

----, A.J. Faulks, H.M Pratt, and B.J. Miflin. 1978. The varietal identification of single seeds of wheat by sodium dodecyl-sulphate polyacrylamide gel electrophoresis of gliadin. J. Sci. Food Agric. 29:847–849.

----, J.M. Field, A.J. Faulks, S. Parmar, B.J. Miflin, M.D. Dietler, E.J.-L. Lew, and D.D. Kasarda. 1984. The purification and N-terminal amino acid sequence analysis of the high molecular weight gluten polypeptides of wheat. Biochim. Biophys. Acta 788:23–34.

----, ----, E.J.-L. Lew, and D.D. Kasarda. 1982. The purification and characterization of two groups of storage proteins (secalins) from rye (*Secale cereale* L.). J. Exp. Bot. 33:261–268.

Simeone, R., A. Blanco, and B. Giorgi. 1983. The primary trisomics of durum wheat (*Triticum durum* Desf.). p. 1103–1107. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet.

Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University.

Singh, R.J., and T. Lelley. 1975. Giemsa banding in meiotic chromosomes of rye, *Secale cereale* L. Z. Pflanzenzuecht. 75:35–89.

----, and G. Röbbelen. 1975. Comparison of somatic Giemsa banding patterns in several species of rye. Z. Pflanzenzuecht 75:270–285.

----, and ----. 1976. Giemsa banding technique reveals deletions within rye chromosomes in addition lines. Z. Pflanzenzuecht 76:11–18.

----, and T. Tsuchiya. 1982. Identification and designation of telocentric chromosomes in barley by means of Giemsa N-banding technique. Theor. Appl. Genet. 64:13–24.

Singh, R.P., and R.A. McIntosh. 1984. Complementary genes for reaction to *Puccinia recondita tritici* in *Triticum aestivum*. I. Genetic and linkage studies. Can. J. Genet. Cytol. 26:723–735.

Smith, A.G., and J.C. Gray. 1984. Localization of the gene for the P700 - chlorophyll *a* protein in chloroplast DNA from pea and wheat. Biochem. Soc. Trans. 12:272–273.

Smith, D.B., and R.B. Flavell. 1975. Characterisation of the wheat genome by renaturation kinetics. Chromosoma 50:223–242.

----, and ----. 1977. Nucleotide sequence organisation in the rye genome. Biochim. Biophys. Acta 474:82–97.

Smithies, O. 1955. Zone electrophoresis in starch gels: Group variations in the serum proteins of normal human adults. Biochem. J. 61:629–641.

Snape, J.W., C.N. Law, and A.J. Worland. 1975. A method for the detection of epistasis in chromosome substitution lines of hexaploid wheat. Heredity 34:297–303.

Southern, E. 1975. Detection of specific sequences among DNA fragments separated by gel electrophoresis. J. Mol. Biol. 98:503–517.

Sozinov, A.A., and F.A. Poperelya. 1980. Genetic classification of prolamines and its use for plant breeding. Ann. Technol. Agric. 29:229–245.

Spencer, D.F., L. Bonen, and M.W. Gray. 1981. Primary sequence of wheat mitochondrial 5S ribosomal ribonucleic acid: Functional and evolutionary implications. Biochem. 20:4022–4029.

----, M.N. Schnare, and M.W. Gray. 1984. Pronounced structural similarities between the small subunit ribosomal RNA genes of wheat mitochondria and *Escherichia coli*. Proc. Natl. Acad. Sci. USA 81:493–497.

Spiker, S. 1982. Histone variants in plants. Evidence for primary structure variants differing in molecular weight. J. Biol. Chem. 257:14250–14255.

----. 1984a. Chromatin structure and gene regulation in higher plants. Adv. Genet. 22:145–208.

----. 1984b. High mobility group chromosomal proteins of wheat. J. Biol.Chem. 259:12007–12013.

----, and J.L. Key. 1976. Identification and fractionation of plant histones. Arch. Biochem. Biophys. 176:510–518.

----, J.K.W. Mardian, and I. Isenberg. 1978. Chromosomal HMG proteins occur in three eukaryotic kingdoms. Biochem. Biophys. Res. Commun. 82:129–135.

----, M.G. Murray, and W.F. Thompson. 1983. DNase I sensitivity of transcriptionally active genes in intact nuclei and isolated chromatin of plants. Proc. Natl. Acad. Sci. USA 80:815–819.

Stack, S. 1982. Two-dimensional spreads of synaptonemal complexes from Solanaceous plants. I. The technique. Stain Technol. 57:265–272.

Stegemann, H., and G. Pietsch. 1983. Methods for characterization of the seed proteins in cereals and legumes. p. 45–75. *In* W. Gottschalk and H.P. Muller (ed.) Seed proteins—Biochemistry, genetics, nutritional value. M. Nijhoff, Dan Haag, Netherlands.

Steinitz-Sears, L.M. 1966. Somatic instability of telocentric chromosomes in wheat and the nature of the centromere. Genetics 54:241–248.

Stern, D.B., and J.D. Palmer. 1984. Extensive and widespread homologies between mito-

chondrial DNA and chloroplast DNA in plants. Proc. Natl. Acad. Sci. USA 81:1946–1950.

Suseelan, K.N., M.V.P. Rao, C.R. Bhatia, and I.N. Rao. 1982. Mapping of an alcohol dehydrogenase (*Adh-A1*) structural gene on chromosome 4A of durum wheat. Heredity 49:353–357.

Sybenga, J. 1983. Rye chromosome nomenclature and homoeology relationships workshop report. Z. Pflanzenzuecht. 90:297–304.

Tabata, T., K. Sasaki, and M. Iwabuchi. 1983. The structural organization and DNA sequence of a wheat histone H4 gene. Nucleic Acids Res. 11:5865–5875.

Tang, K.S., and G.E. Hart. 1975. Use of isozymes as chromosome markers in wheat–rye addition lines and in triticale. Genet. Res., 26:187–201.

Tanksley, S.D. 1983. Gene mapping. p. 109–138. *In* S.D. Tanksley and T.J. Orton (ed.) Isozymes in plant genetics and breeding, Part A. Elsevier Science Publishers B.V., Amsterdam.

Teoh, S.B., and J. Hutchinson. 1983. Interspecific variation in C-banded chromosomes of diploid *Aegilops* species. Theor. Appl. Genet. 65:31–40.

----, ----, and T.E. Miller. 1983a. A comparison of the chromosomal distribution of cloned repetitive DNA sequences in different *Aegilops* species. Heredity 51:635–641.

----, T.E. Miller, and S.M. Reader. 1983b. Intraspecific variation in C-banded chromosomes of *Aegilops comosa* and *Ae. speltoides*. Theor. Appl. Genet. 65:343–348.

The, T.T., and E.P. Baker. 1973. Misdivision of an *Agropyron elongatum* chromosome. Wheat Inf. Serv. 36:19–20.

----, and R.A. McIntosh. 1975. Cytogenetical studies in wheat. VIII. Telocentric mapping and linkage studies involving *Sr22* and other genes in chromosome 7AL. Aust. J. Biol. Sci. 28:531–538.

Thoma, F., and T.H. Koller. 1977. Influence of histone H1 on chromatin structure. Cell 12:101–107.

Thomas, J.B., and P.J. Kaltsikes. 1974. A possible effect of heterochromatin on chromosome pairing. Proc. Natl. Acad. Sci. USA 71:2787–2790.

Thompson, R.D., D. Bartels, N.P. Harberd, and R.B. Flavell. 1983. Characterization of the multigene family coding for HMW glutenin subunits in wheat using cDNA clones. Theor. Appl. Genet. 67:87–96.

Timischl, W., and J. Greilhuber. 1983. Estimation of relative DNA density in heterochromatin from C-band karyotypes. Heredity 51:665–668.

Timmis, J.N., and N.S. Scott. 1984. Promiscuous DNA: Sequence homologies between DNA of separate organelles. Trends Biochem. Sci. 9:271–273.

Tkachuk, R., and J. Mellish. 1980. Wheat cultivar identification by high voltage gel electrophoresis. Ann. Technol. Agric. 29:207–212.

Tsunewaki, K. 1966. Comparative gene analysis of common wheat and its ancestral species. II. Waxiness, growth habit and awnedness. Jpn. J. Bot. 19:175–229.

---- (ed.) 1980. Genetic diversity of the cytoplasm in *Triticum* and *Aegilops*. Japanese Society for the Promotion of Science, Tokyo.

----, and E.G. Heyne. 1960. The transmission of the monosomic condition in wheat var. Chinese Spring. J. Heredity 51:63–68.

----, and Y. Ogihara. 1983. The molecular basis of genetic diversity among cytoplasms of *Triticum* and *Aegilops* species. II. On the origin of polyploid wheat cytoplasms as suggested by chloroplast DNA restriction fragment patterns. Genetics 101:155–171.

Unrau, J. 1950. The use of monosomes and nullisomes in cytogenetic studies of common wheat. Sci. Agric. 30:66–89.

Upadhya, M.D., and M.S. Swaminathan. 1967. Mechanisms regulating chromosome pairing in *Triticum*. Biol. Zentralbl. 87(Suppl.):239–255.

Van Niekerk, H.A., and R. de V. Pienaar. 1983. Morphology and linear C-band differentiation of *Triticum aestivum* L. em. Thell. v. *aestivum* cv. 'Chinese Spring' chromosomes. Cereal Res. Commun. 11:115–122.

Vardi, A. 1973. Introgression between different ploidy levels in the wheat group. p. 131–

144. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Vedel, F., P. Lebacq, and F. Quetier. 1980. Cytoplasmic DNA variation and relationships in cereal genomes. Theor. Appl. Genet. 58:219–224.

----, F. Quetier, and M. Bayen. 1976. Specific cleavage of chloroplast DNA from higher plants by EcoRI restriction nuclease. Nature (London) 263:440–442.

----, ----, Y. Cauderon, F. Dosba, and G. Doussinault. 1981. Studies on maternal inheritance in polyploid wheats with cytoplasmic DNAs as genetic markers. Theor. Appl. Genet. 59:239–245.

----, ----, F. Dosba, and G. Doussinault. 1978. Study of wheat phylogeny by EcoRI analysis of chloroplastic and mitochondrial DNAs. Plant Sci. Lett. 13:97–102.

Verma, S.C., and H. Rees. 1974. Giemsa staining and the distribution of heterochromatin in rye chromosomes. Heredity 32:118–121.

Vosa, C.G. 1974. The basic karyotype of rye (*Secale cereale*) analyzed with Giemsa and fluorescence methods. Heredity 33:403–408.

Wagenaar, E.B. 1961. Studies on the genome constitution of *Triticum timopheevi* Zhuk. I. Evidence for genetic control of meiotic irregularities in tetraploid hybrids. Can. J. Genet. Cytol. 3:47–60.

Wagner, I., and I. Capesius. 1981. Determination of 5-methyl-cytosine from plant DNA by high-performance liquid chromatography. Biochim. Biophys. Acta 654:52–56.

Waines, J.G. 1976. A model for the origin of diploidizing mechanisms in polyploid species. Am. Nat. 110:415–430.

Wall, A.M., R. Riley, and M.D. Gale. 1971. The position of a locus on chromosome 5B of *Triticum aestivum* affecting homoeologous meiotic pairing. Genet. Res. 18:329–339.

Wall, J.S. 1979. The role of wheat proteins in determining baking quality. p. 275–311. *In* D.L. Laidman and R.G. Wyn Jones (ed.) Recent advances in the biochemistry of cereals. Academic Press, London.

Wehling, P., G. Schmidt-Stohn, and G. Wricke. 1985. Chromosomal location of esterase, peroxidase, and phosphoglucomutase isozyme structural genes in cultivated rye (*Secale cereale* L.). Theor. Appl. Genet. 70:377–382.

Wehr, C.T. 1984. Commercially available HPLC columns for chromatography of proteins, peptides, and amino acids. p. 31–57. *In* W.S. Hancock (ed.) Handbook of HPLC for the separation of amino acids, peptides, and proteins, Vol. I. CRC Press, Boca Raton, FL.

Welsh, J.R., and E.R. Hehn. 1964. The effect of chromosome 1D on hexaploid wheat flour quality. Crop Sci. 4:320–323.

Westcott, B., M.D. Gale, and J.A. McVittie. 1978. A comparison of backcross and selfing methods for telocentric mapping in wheat. Heredity 40:59–66.

Whitby, A.J., P.R. Stone, and W.J.D. Whish. 1979. Effect of polyamines and Mg^{++} on poly (ADP-Ribose) synthesis and ADP-ribosylation of histones in wheat. Biochem. Biophys. Res. Commun. 90:1295–1304.

Willey, D.L., C.J. Howe, A.D. Auffret, C.M. Bowman, T.A. Dyer, and J.C. Gray. 1984. Location and nucleotide sequence of the gene for cytochrome *f* in wheat chloroplast DNA. Mol. Gen. Genet. 194:416–422.

Williams, N.D., and S.S. Maan. 1973. Telocentric mapping of genes for resistance to stem rust of wheat. p. 765–770. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genetics Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Windemann, H., F. Fritschy, and E. Baumgartner. 1982. Enzyme-linked immunosorbent assay for wheat α-gliadin and whole gliadin. Biochim. Biophys. Acta 209:110–121.

Wolf, G., and J. Rimpau. 1979. Structural and regulatory genes for phosphodiesterase in wheat. p. 705–712. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Ind. Soc. Genet. Plant Breeding, Ind. Agric. Res. Inst., New Delhi.

----, ----, and T. Lelley. 1977. Localization of structural and regulatory genes for phosphodiesterase in wheat (*Triticum aestivum*). Genetics 86:597–605.

Woychik, J.H., J.A. Boundy, and R.J. Dimler. 1961. Starch gel electrophoresis of wheat gluten proteins with concentrated urea. Arch. Biochem. Biophys. 94:477–482.

Wrigley, C.W. 1968. Gel electrofocusing—A technique for analyzing multiple protein samples by isoelectric focusing. Sci. Tools 15:17–23.

----. 1970. Protein mapping by combined gel electrofocusing and electrophoresis: Application to the study of genotypic variations in wheat gliadins. Biochem. Genet. 4:509–516.

----. 1982. The use of genetics in understanding protein composition and grain quality in wheat. Qual. Plant. Plant Foods Hum. Nutr. 31:205–227.

----, J.-C. Autran, and W. Bushuk. 1982a. Identification of cereal varieties by gel electrophoresis of the grain proteins. Adv. Cereal Sci. 5:211–259.

----, G.J. Lawrence, and K.W. Shepherd. 1982b. Association of glutenin subunits with gliadin composition and grain quality in wheat. Aust. J. Plant Physiol. 9:15–30.

----, P.J. Robinson, and W.T. Williams. 1981. Association between electrophoretic patterns of gliadin proteins and quality characteristics of wheat cultivars. J. Sci. Food Agric. 32:433–442.

----, ----, and W.T. Williams. 1982c. Associations between individual gliadin proteins and quality, agronomic and morphological attributes of wheat cultivars. Aust. J. Agric. Res. 33:409–418.

----, and K.W. Shepherd. 1973. Electrofocusing of grain proteins from wheat genotypes. Ann. N.Y. Acad. Sci. 209:154–162.

Zhao, Y.H., and G. Kimber. 1984. New hybrids with D-genome wheat relatives. Genetics 106:509–515.

Zohary, D., and M. Feldman. 1962. Hybridization between amphidiploids and the evolution of polyploids in the wheat (*Aegilops–Triticum*) group. Evolution 16:44–61.

Zurabishvili, T.G., A.B. Iordansky, and N.S. Badaev. 1974. Polykaryogram analysis and the investigation of differential staining of *Triticum aestivum* chromosomes. Dokl. Akad. Nauk. SSSR 218:207–210.

----, ----, and ----. 1978. Linear differentiation of cereal chromosomes. II. Polyploid wheats. Theor. Appl. Genet. 51:201–210.

6 Management of the Wheat Crop

Billy Tucker, *coordinator*

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J. H. Stiegler

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6 Management of the Weat Crop

Billy Tucker, ***coordinator***

This chapter deals with the actual production of the wheat crop. Important principles and general practices are presented. Since specific cultural practices vary greatly between areas, it is beyond the scope of this monograph to address specific production practices for all wheat growing areas. Many good combinations of practices are available for wise utilization of resources and to maximize profits. The seven sections in this chapter discuss important phases of wheat production not covered elsewhere in this monograph.

Management practices for wheat production are changing, and with these changes have come higher yields and improved quality. Improved management practices are aimed toward increased production efficiency. Much has been learned about wheat production management. Research is continuing on wheat production management, providing a large storehouse of vital information; however, much remains to be learned, and as new discoveries are made, production practices will continue to change.

The greatest opportunity for improved wheat production efficiency is likely to result from an integration of all important cultural practices into complete management packages.

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6A Cropping Systems and Rotations

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A cropping system is a system of crop production that makes maximum use of resources to ensure a reasonable profit while also protecting or conserving the resources. It explains the what, why, and how for a crop grown in a particular area (Chapman and Carter, 1976, ch. 10). Some systems are fairly easy to describe. The wheat (*Triticum aestivum* (L.)-fallow system typical of cereal production in semiarid areas of the United States where wheat is rotated with a fallow every other year is a good example. Where climates and soils are more favorable for crop production, systems are more complex because there are more crop choices. Intercropping, double-cropping, and even triple-cropping are workable modifications to many basic cropping systems for wheat.

Generally cropping systems in a particular area are used because they work best and have a potential for profit. They are used either to prevent problems, such as pests, or to solve existing ones, such as saline seeps. For much of the major wheat production area, cropping systems that emphasize moisture conservation and storage are critical. Other considerations include climate, soil and topography, pests, markets, transportation, and government programs.

Crop rotation, practiced by early wheat producers, continues to be important but is only one part of the cropping system. Definite crop rotations are not a part of the farming practices in the important wheat-producing areas, due mainly to climatic hazards and the lack of a crop that can compete with wheat. Even so, rotation offers producers easier control of diseases, insects, and weeds, allows for increased yields, and helps ensure crop stability. Rotation with legumes allows for increased soil N and improved soil physical conditions; however, legume rotation often removes valuable moisture for cash crop production.

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6A–1 SYSTEMS AND ROTATIONS UNDER SEMIARID CONDITIONS

6A–1.1 Pacific Northwest

Cropping systems in the Pacific Northwest are diverse and are dependent on the amount of annual precipitation. Alternating winter wheat and fallow is the most common system in the dry-farmed areas. Where precipitation ranges from 330 to 400 mm, two or three crops are grown between fallow periods. The intensity is dependent on yearly precipitation, with a rotation of fallow-winter wheat-spring small grain in sequence. Reduced and no-till practices have extended the annual cropping interval westward and permit a winter wheat–spring wheat–lentil (*Lens culinaris* Medik.) rotation where the wheat is planted no-till after the lentil harvest. These systems conserve more moisture and reduce soil erosion over fallowing (Engle et al., 1982).

Annual cropping of winter wheat-spring wheat or barley-peas (*Hordeum vulgare* L.) and (*Pisum sativum* L.) or lentil in rotation is readily practiced where precipitation exceeds 450 mm. Spring crops are used for grassy weed control and winter wheat always follows pea or lentil. A crop rotation that includes legume–grass sod is more effective for erosion control and produces higher wheat yields than fallow–wheat systems on steeply sloping land such as in the Palouse.

6A–1.2 Northern Great Plains

In the northern Great Plains, water conservation is essential and summer fallowing is included in nearly all cropping systems. Reducing evaporation and retaining precipitation where it falls is especially important with snow. Both spring and winter wheat are grown in a crop–fallow rotation; however, the fallow is 21 months for spring wheat and 14 months for winter wheat, or 2 yr to produce one crop (Willis, 1976). Another common practice is to follow maize (*Zea mays* L.) or other cultivated crops with spring wheat. Haas et al. (1974a), from a study of 14 northern Great Plains locations, found that spring wheat yields were higher when wheat followed maize than when wheat followed wheat. Small wheat yield differences after maize suggest that maize might be a good substitute for fallow. The reason for the small differences is that even with fallow over two winters, water storage efficiencies are usually $< 25\%$. Other crop rotations include wheat–flax, (*Linum usitatissimum* L.) wheat–barley, and wheat–sunflower (*Helianthus annuus* L.)–fallow. Grasses and legumes have been used in rotations, but in these moisture-deficient areas they tend to dry out the soil. In years when moisture is not limiting, wheat yields after legumes were 50% better than when a nonlegume was used (Stoa and Zubriski, 1969).

No-till planting of winter wheat into standing stubble in North Dakota is adding flexibility for growers (Ball and Larsen, 1985). Winter

wheat survival has been greatly improved. Snow trapped by the stubble provided 2.5 cm of water when compared with fields conventionally planted (Black and Siddoway, 1977b). While yields have not been as good as for spring wheat, labor distribution at planting and harvesting are advantages to spring wheat-winter wheat rotation.

6A–1.3 Southern Great Plains

Definite crop rotations are not an established part of the farming practices of the southern Great Plains. Wheat usually follows wheat, mainly because of the lack of a suitable successful alternative. Also, wheat is recognized as a high-quality forage. Annual cropping to produce forage is usually achievable and its value in terms of pounds of beef often exceed its value as grain (Donnelly and McMurphy (1983). Wheat–graze out or wheat–hay are the only modifications to continuous wheat systems in this region. Except for the short summer fallow between harvest in June and seeding in fall, fallowing is practiced only the extreme west, where it does increase wheat yields on the harvested acres. Some economic benefits from farming fewer acres and added farming system stability are cited reasons for fallow. Fryrear (1976) reported that continuous wheat yields were 82.5% of fallow yields at six locations over 64 treatment years. At Bushland, TX, continuous wheat yields were 73% of 1-yr fallow. Continuous wheat yields for the Magruder plots at Oklahoma State University (annual cropping since 1893) have not declined (Webb et al., 1980).

A wheat–sorghum–fallow (WSF) rotation is used successfully in the Texas Panhandle, parts of Oklahoma, and the 500 to 700 mm rainfall area in Kansas. The sequence results in two crops in 3 yrs with an 11-month fallow between crops. Unger (1972) found wheat yields in the WSF rotation were not markedly different from wheat yields in wheat–fallow systems. Similar trends also were found to occur in Kansas. Grain sorghum yields in the WSF system were 27% greater than continuous sorghum yields over a 13-yr period. Norwood (1984), in studies started in 1973, expanded a WSF rotation study to include reduced and no-till treatments. Grain sorghum response ranged from -5 to 44 kg/ha.

Fallowing is a proven, economical, and necessary cropping system practice for most of the wheat-producing area of the central Great Plains (Fenster et al., 1969; Fenster and McCalla, 1970; Greb, 1979; Smika, 1970).The wheat-fallow system is used by the majority of dryland farmers where annual precipitation is < 450 mm. Water storage efficiencies and crop yields from wheat-fallow systems are better in this region than similar practices elsewhere. Hays (1982) reported on 188 crop years of studies in Kansas, Nebraska, and Colorado, where fallow wheat yields averaged 2.0 to 2.5 times higher than continuous wheat yields.

Improvements in tillage and planting, tools, minimum and no-till techniques, and weed control practices have led to better residue management and more effective wind and water erosion control. This has further improved water storage and has been responsible for increasing

crop yield in the wheat-fallow region. Wicks and Smika (1973) compared five fallow treatments and found that no-tillage had the highest grain yield, less weeds, and more stored soil moisture than any of the other fallow treatments.

6A–1.4 Central Great Plains

The eastern part of the central Great Plains wheat region is generally cropped annually. Wheat is grown on a continuous basis but is often rotated with grain sorghum, [*Sorghum bicolor* (L.) Moench] maize, and soybean [Glycine max (L.) Merr.]. Significant hectares of double-cropped wheat and soybean are also grown.

Between the humid east and the semiarid west is a *fallow transition* zone. This area generally receives ample precipitation for annual cropping but is usually fallowed. Some continuous wheat is grown, but the major cropping system is wheat–sorghum–fallow. The system provides farmers with the flexibility to react to erratic precipitation conditions. If the fall is too dry to plant wheat, the grower can wait and plant grain sorghum in the spring. It is difficult to get back to wheat, however, and usually there is an 11-month fallow after grain sorghum (Greb et al., 1974).

The practice of *eco-fallow*, a no-till, chemical fallow cropping system that relies heavily on herbicides, is gaining acceptance in this region. The typical cropping system is winter wheat–grain sorghum, maize or millet–fallow. The system has four crops in 6 yr; the summer crop allows for disrupting insect, disease, and weed cycles.

6A–2 SYSTEMS AND ROTATIONS UNDER HUMID CONDITIONS

Ample moisture and favorable temperatures and growing conditions in much of the eastern United States make wheat as a continuous crop less profitable than other grains. Winter wheat does serve as a good cover crop to reduce leaching and to control erosion. In many years it can be valuable for pasture, either clean tilled or overseeded into bermudagrass in the Southeast. Winter wheat is well suited as a companion crop for clover (*Trifolium* spp.) and alfalfa (*Medicago sativa* L.) and fits well into rotations that use legumes and row crops (Reitz, 1976). Although numerous other rotations use wheat as part of the scheme (most often wheat–maize–soybean and oats (*Avena sativa* L.) are used. In the South, grain sorghum and cotton are included in rotations.

By far the most widespread use of wheat in this region is in double-cropping systems. A 3-yr Alabama study using conventional tilled double-cropped soybean produced only slightly less yield than single-cropped soybean. Rogers et al., (1971) and Sanford et al. (1973) found that wheat–soybean double-cropping produced higher net returns than wheat–grain sorghum. Gallaher (1975) demonstrated the feasibility of double-cropping

two silage crops or one silage and one grain crop per year using wheat. In North Carolina, a 3-yr sequence of wheat–maize, wheat–grain sorghum, and wheat–soybean did not produce as much net return as double-crop wheat–soybean. A 2-yr sequence of wheat–no-till soybean–no-till maize did compare favorably (Lewis and Phillips, 1976).

6B Soil Management—Tillage, Seedbed Preparation, and Erosion Control

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Modern-day tillage, seedbed preparation, and erosion control practices for wheat [*Triticum aestivum* (L.)] production in the semiarid and subhumid climates of the North American Great Plains and the Pacific Northwest have evolved predominately from experiences and research results obtained in wheat-fallow cropping systems. Recent innovations in wheat culture using double cropping, with or without tillage, and the use of no-till summer fallow are being developed. However, the majority of all wheat in North America is grown on land that has been fallowed and tilled some time before or at the time of seeding. Even if wheat is grown in conjunction with other cereal grain and oilseed crops in extended 3- or 4-yr rotations, fallow is usually included and reserved for planting to wheat (Haas et al., 1974b).

Because of the importance of quality of fallow systems to the sustained production of wheat, the basic objectives of fallowing have been defined and upgraded as a result of years of research and experience. The objectives of fallowing are as follows: (i) maximize soil water storage and control seedbed soil water sufficient to establish and produce a wheat crop; (ii) maximize plant nutrient availability (N); (iii) minimize soil erosion hazards (residue and soil clod management); and (iv) minimize energy and economic inputs.

Fallow systems have evolved through the periodic introduction of improved equipment and new knowledge, as exemplified by the historical

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data assembled by Greb (1979) for the U.S. Central Great Plains Field Station (Table 6B–1).

As fallow systems improved, the capacity to retain straw mulches and control weeds more efficiently during the entire summer fallow period gradually improved. This resulted in increased soil water storage, grain yields, and water-use efficiency. Intensive tillage systems with moldboard plowing, harrowing, and disking have given way gradually to chisel, sweep, and undercutting tillage systems, accompanied recently by an increase in the use of herbicides; these herbicides may reduce or eliminate the need for tillage operations. Controlling weeds by tillage and/or herbicides during fallow conserves soil water and usually reduces weed populations during the cropping season. (Weed control is discussed in detail in section 6G.)

Cultural practices have evolved because of the unique relationship between tillage and crop residue management with respect to their effect on soil properties that influence water conservation and vulnerability to wind and water erosion. However, the effectiveness of any tillage and crop residue management system is subject to the vagaries of climate extremes, and overall effectiveness is often site specific, due to soil texture, field slope length, crops grown, quantity of crop residue produced, and other soil and crop management factors.

Tillage and crop residues influence soil aeration, water relations, temperature, and various other physical, chemical, and biological properties that collectively govern seedzone and plant root environments. Early tillage experiments provided important soil and water conservation information about a specific tillage system, but not about the independent influence of cropping sequence, residue management, and tillage on soil properties (McCalla and Army, 1961; Zingg and Whitfield, 1957). This problem was recognized by Mathews (1945) when he stated, "Comparison of soil structure between land with and without residues on the soil surface is complicated by the fact that different tillage implements are used." Later investigations defined and clarified the independent role of crop residues for enhancing soil water storage and improving soil properties within a given tillage treatment (Greb et al., 1970; Black, 1973a, 1973b). Progress has been made in isolating the primary factors influencing the chemical and physical properties of soil in wheat culture systems.

6B–1 TILLAGE EFFECTS ON SOIL PROPERTIES

Selection of a tillage implement should be based on what soil physical condition the operator is seeking and on how much surface residue is needed to protect against soil erosion. Extensive information on surface residue conservation (or reduction) in relation to tillage implements, speed and depth of operation, and crop residue characteristics is available (Anderson, 1961, 1964, 1965, 1967, 1968; Smika, 1976a; Woodruff et al., 1977).

Table 6B–1. Progress in summer fallow systems and wheat yields, U.S. Central Great Plains Research Station, Akron, CO (Greb, 1979).

Years	Progress in fallow systems	Average annual precipitation	Drought years	Fallow water storage†	Percent fallow efficiency	Wheat yield	Water-use efficiency‡
		mm	no.	mm	%	kg ha^{-1}	kg ha^{-1} per mm
1916–30	Maximum tillage; plow harrow (dust mulch)	439	1	101	19	1070	1.2
1931–45	Conventional tillage; shallow disk, rodweeder	401	5	112	24	1160	1.4
1946–60	Improved conventional tillage; begin stubble mulch 1957	416	3	137	27	1730	2.1
1961–75	Stubble mulch; begin minimum tillage with herbicides 1969	389	4	157	33	2170	2.8
1976–90	Projected estimate. Minimum tillage; begin no-till 1983	412§	3	183	40	2690	3.3

†Based on 14 months fallow, mid-July to second mid-September.
‡Assuming 2 yrs precipitation per crop in a wheat-fallow system.
§Assuming average precipitation from 1976 to 1990.

Information on the effects of tillage alone (with no residue variable) on soil water relationships and soil properties is limited. In the central and northern Great Plains, fall tillage that flattens or buries crop residues reduces snow trapping, which subsequently decreases soil water storage (Black and Power, 1965; Black and Siddoway, 1976, 1977b; Greb et al., 1970). Fall chiseling in combination with no-till fallow or mechanical fallow increases potential infiltration rates by changing the hydraulic properties and soil water desorption characteristics of a soil, which may influence soil water relations (Allmaras et al., 1977; Barnes and Bohmont, 1958). Summer fallowing when crop residue quantities are relatively low (2000 kg ha $^{-1}$ or less) requires an early June tillage to conserve additional soil water compared to no-till fallow (Black and Power, 1965). During hot summer or drought periods, tillage is needed to interrupt capillary movement of soil water to the surface for subsequent evaporation (Black and Power, 1965; Papendick et al., 1973). In the absence of surface residue, a soil mulch layer created with a rodweeder operated at rather precise soil depths decreased evaporation rate and controlled the positional availability of water, as needed for germination of wheat following extended dry periods (Papendick et al., 1973). Therefore, when the quantity of wheat residue available at the beginning of fallow is low (0 to 2000 kg ha $^{-1}$), tillage effects on soil water relations may become more pronounced. Laboratory simulation of tillage at 1.5- and 7.5-cm soil depths, with no surface residue present, essentially terminated the first or constant-rate stage of drying, with a 60% reduction in evaporation over a 15-day period compared to an undisturbed soil column (Willis and Bond, 1971).

Initial or primary tillage at the beginning of a cropping or fallow season usually improves soil structure (porosity and roughness). Type of tillage implement used has a decided influence on size and stability of soil clods formed (Lyles and Woodruff, 1962). Differences in clod stability associated with different tillage implements persisted longer than those due to soil water content at time of tillage, particularly for intermediate soil water conditions. The moldboard plow produced the most stable aggregates initially, followed by the one-way disk plow, then sweep tillage. For soils without surface residue, Smika and Greb (1975) found that aggregation at the end of summer fallow decreased in order when tilled by chisel, wide blade, sweep cultivator, and disk implements. Under conditions of very low spring wheat residue levels on a sandy soil, dry aggregate stability decreased in order for summer fallow tillage treatments of chisel plus wide blade, wide blade, one-way, and moldboard plow (Power et al., 1958).

Climate and soil conditions frequently have a dominant influence on surface soil properties independent of the tillage implement used. One-way sweep and delayed sweep tillage produced no consistent differences in dry aggregates greater than 0.84 mm in diameter in a long-term study (Unger, 1982), and the quantity of nonerodible soil aggregates was in-

sufficient to control wind erosion on a bare-smooth soil surface. Tillage interval or number of tillage operations performed with a sweep cultivator during summer fallow after an early spring moldboard plowing had no significant effect on mean-weight diameter of soil aggregates (Bauer and Conlon, 1974). However, as the summer fallow season progressed, mean-weight diameter of soil aggregates decreased from 18.3 mm on 3 June to 9.0 mm on 24 October as a result of climatic factors independent of interval between, or frequency of, tillage operations.

Larson and Gill (1973) discussed some important characteristics of the structure of the tilled layer and degradation of tilled soil structure, as well as principles for managing tilled soil structure. Tillage systems alter surface roughness and porosity (bulk density). Aside from influencing the energy balance at the soil surface, roughness and porosity also influence water detention and infiltration. Soil roughness is the primary factor influencing initial infiltration of water from simulated rainfall, before runoff occurs (Burwell and Larson, 1969) (Table 6B–2). Differences in soil porosity, alone or in combination with surface roughness, had only minor effects on infiltration. During a 50-mm runoff event that followed, cumulative infiltration of water was not influenced by initial soil roughness or porosity differences.

Surface soil roughness, stability of soil clods, and aggregate structure influence infiltration. Excessive tillage degrades soil structure stability, which renders the soil more susceptible to particle dispersion by rain (surface sealing), to development of soil crusts with high soil strength, and to transport of finely divided soil particles by wind and water (Larson and Gill, 1973).

6B–2 TILLAGE FOR SEEDBED PREPARATION

Tillage may be necessary to control seedzone soil water content and other soil environmental properties required for seed germination and plant establishment when insufficient crop residue is present, during prolonged periods of drought, or when the soil must be sufficiently dried to

Table 6B–2. Tillage effects on cumulative infiltration in Barnes loam (Burwell and Larson, 1969).†

Tillage treatment	Surface condition		Cumulative infiltration	
	Pore space	Random roughness	To initial runoff	During 50-mm runoff
	mm			
Untilled	80	6	9 a‡	21 a
Plow	139	57	93 c	21 a
Plow-disk-harrow	106	15	24 a	21 a
Cultivated	113	35	67 b	24 a
Rotary tilled	129	17	48 b	21 a

†Simulated rainfall applied at a rate of 127 mm hg^{-1}.
‡Column values not followed by same letter are significantly different ($P = 0.05$).

permit planting within a desirable time frame on fine-textured soils. Hammel et al. (1981) developed a numerical model to investigate the dynamic aspects of heat and water flow in the upper soil layer, with emphasis on the effects of conventional-tillage and no-till fallow on these processes and ultimately on seedzone water content. Papendick et al. (1973) illustrated the rather precise tillage depth requirements for primary blade-tillage and secondary rodweeder tillage in maintaining sufficient seedzone water concentrations at the end of fallow to obtain satisfactory winter wheat germination and stand. As summer drought periods during fallow approach 90 days, insufficient seedzone water would be present to effect seed germination, even with residue present (Hammel et al., 1981). In annual cropping of spring wheat, Bauer and Kucera (1978) investigated the influence on some seedzone soil properties of fall tillage (blade, double disk, moldboard plow, and no-till) upon which were superimposed spring tillages involving the same treatments as the fall tillage but including also a cultivator with harrow attachment treatment. In general, soil property differences were greater between years (because of annual variations in climate, quantity of residue present at time of tillage, and soil water content at time of tillage) than the differences produced by tillage treatments in a given year. Bulk densities were usually lowest for moldboard plow and highest for no-till, but water concentration in the 0- to 15-cm depth was highest with no-till and lowest with plowing. Tillage effects on plant populations and grain yields were inconsistent and not significantly related to any of the soil properties measured over a period of years because tillage effects themselves were inconsistent among years.

In subhumid climates on somewhat poorly drained, fine-textured soils such as North Dakota's Red River Valley and some northern Corn Belt soils, excess soil water can delay seeding in more than 50% of the years (Bauer and Kucera, 1978). The management approach is to moldboard plow the land in the fall, to eliminate snow accumulations and to hasten spring drying and thus to facilitate timely spring tillage and seeding operations.

6B–3 CROP RESIDUE EFFECTS

In semiarid regions where additional soil water usually increases crop yields, proper management of crop residues on the soil surface in a cropping system enhances water storage in the soil profile (Brawand, 1964; Black, 1973a; Greb et al., 1970; Smika, 1976a; Lindwall and Anderson, 1981; Unger and Wiese, 1979) and seedzone soil water content (Army et al., 1961; Smika, 1976b). An important aspect of crop residue management in regions of winter snowfall is stubble orientation. Untilled upright wheat stubble traps and holds snow on the land. In a 4-yr study, Smika and Whitfield (1966) reported an average overwinter gain in soil water storage of 52 mm in untilled stubble, compared to an average loss of 3 mm when wheat stubble was incorporated with a one-way disk in the

fall. Staple et al. (1960) found that 37% of winter precipitation was conserved as stored soil water in untilled wheat stubble, compared with only 9% when soil surface was void of stubble.

Small amounts of crop residue on the soil surface will reduce water loss during first-stage evaporation (Bond and Willis, 1969) but large quantities (3000 kg ha^{-1} or more) are required to save significant amounts of soil water for extended periods of time (Bond and Willis, 1971; Smika, 1976b). After a 34-day drying cycle, wheat residue levels of 1200, 2200, and 3700 kg ha^{-1} associated with tillage only, reduced-tillage, and no-till fallow treatments, respectively, had adequate seedzone water concentration for winter wheat germination at 14-, 12-, and 7-cm soil depths, respectively (Smika, 1976b). Surface residues generally reduce spring and summer soil temperatures (Allmaras et al., 1973; Taylor, 1967), which in turn influences soil N mineralization (Stanford et al., 1973; McCalla and Russel, 1943; Smika et al., 1969). However, the combined effect of a wheat straw mulch on soil water and temperature can be used advantageously in a semiarid climate (Allmaras et al., 1973; Black, 1970; Unger and Wiese, 1979). By manipulating quantity and position of wheat straw between or on the wheat rows, it was shown that maintaining adequate water in the seed and root zones during early plant growth is more critical to subsequent growth and potential wheat yields than soil temperature during drought periods (Black, 1970).

Surface residues increase water infiltration rates, compared with bare soil (Barnes and Bohmont, 1958; Burwell and Larson, 1969, and reduce evaporation from the soil surface (Army et al., 1961; Black, 1973a; Greb et al., 1970; Smika, 1976a, 1976b). As a result of a lower evaporation rate and a lower soil temperature with mulched soils, soil crusting is reduced (Army et al., 1961; Edwards and Larson, 1969). Within a set tillage variable, crop residue effects on dry aggregate soil structure are positive in relation to stability and aggregate size needed to reduce soil erodibility by wind (Black and Power, 1965; Black, 1973b; Brawand, 1964; Siddoway, 1963; Smika and Greb, 1975), and bulk density of the surface is reduced as residue levels increase (Black, 1973b; Brawand, 1964; Johnson, 1950).

Some long-term cumulative effects of wheat straw residue levels applied at different rates during fallow without a tillage variable on certain physical and chemical properties of soil are shown in Table 6B–3. The positive influence of increasing crop residues on chemical properties of the surface soil include organic matter (Black, 1973b; Ferguson, 1967; Johnson, 1950; Unger, 1968), N (Black, 1973b; Brawand, 1964; Oveson, 1966; Unger, 1968), C (Black, 1973b; Oveson, 1966), available P (Black, 1973b; Johnson, 1950), exchangeable K (Black, 1973b; Ferguson, 1967), and N mineralization by soil incubation (Black, 1973b, Ferguson, 1967). The effects of crop residue levels on some soil chemical properties favor changes toward a progressively higher equilibrium which are proportionate to the quantity of crop residue added over time (Black, 1973b;

Table 6B–3. Cumulative effects of straw residue at different rates during fallow on soil properties in an 8-yr wheat-fallow rotation (Black, 1973b).

Soil property	Residue rate (kg ha $^{-1}$)			
	0	1 680	3 360	6 730
Organic C (%)				
0– 7.6 cm	1.79	1.99	2.11	2.20
7.6–15.2 cm	1.33	1.40	1.50	1.71
15.2–30.5 cm	1.11	1.12	1.25	1.32
Total soil N (%)				
0– 7.6 cm	0.089	0.097	0.096	0.102
7.6–15.2 cm	0.072	0.074	0.083	0.087
15.2–30.5 cm	0.063	0.068	0.069	0.068
N mineralization (mg kg $^{-1}$)†	18.2	20.9	22.7	24.4
$NaHCO_3$ soluble P (mg kg $^{-1}$)	7.8	8.4	8.8	9.6
Exchangeable Ca (mmol kg $^{-1}$)	29.6	29.0	28.2	27.8
Exchangeable K (mmol kg $^{-1}$)	7.1	8.2	9.1	10.1
Erodible fraction (%)‡	50.0	46.0	38.2	27.5
Bulk density				
0– 7.6 cm	1.38	1.31	1.29	1.27
7.6–15.2 cm	1.63	1.58	1.56	1.55
Soil water (cm 1.5 m $^{-1}$)§	14.5	15.5	16.0	18.0

†After 8-week incubation.
‡Surface soil passing 0.84-mm sieve (dry).
§At seeding after 21 months of fallow.

Power and Legg, 1978). Therefore, soil management inputs that increase soil fertility and crop yields also increase the quantity of straw produced and returned to the soil, which in turn is an important aspect in maintaining soil productivity.

6B–4 EROSION CONTROL PRINCIPLES AND PRACTICES

Since the advent of stubble mulch tillage in the Great Plains (Russel, 1976), no one has disputed the value of maintaining crop residues on the soil surface for wind and water erosion control. However, differences in climate and soils in different ecoregions have made it necessary to develop different soil and crop management practices (Dregne and Willis, 1983). Tillage and crop residue management practices that evolved over time to conserve water were developed to be compatible with and to supplement soil resource conservation. The principles of erosion by water (Renard and Foster, 1983) and by wind (Lyles et al., 1983) are known and have been discussed in detail. Of the factors affecting soil loss rates by either wind or water, vegetative cover is the most effective for reducing soil loss (Larson et al., 1978; Skidmore and Siddoway, 1978).

Soil available for transport by inter-rill flow is a function of soil detachment by inter-rill flow, direct raindrop splash impact, and secondary splash impact. Singer et al. (1981) found that the amount of soil moved by rain splash and by inter-rill flow was linearly correlated with surface cover level. With 96% cover of cereal straw, soil loss by splash

transport was reduced to < 8% of that from bare soil and inter-rill transport was only 25% of bare soil. Lyles et al. (1974) collected soil samples to obtain both air-dry and field-moist test clods 12.7 to 38.0 mm in diameter formed by chisel tillage. Soil detachment from similar-size air-dried clods by simulated rainfall was 2.7-fold greater when accompanied by a 11.2 m s^{-1} wind than with no wind. A 50% crop residue cover over the air-dried clods reduced soil detachment by rainfall 63% with no wind and 78% with a 11.2 m s^{-1} wind. With the same residue cover, soil detachment was markedly less from field-moist clods than from air-dried clods of the same size (Lyles et al., 1974).

Initial or primary tillage at the beginning of a cropping or fallow season, when performed at the optimum soil water content, usually improves soil structure (porosity and roughness). This increases water infiltration capacity and the resistance of the soil to wind erosion. Subsequent tillage degrades soil structure and decreases protective vegetative cover, thereby reducing infiltration capacity and increasing the potential for wind erosion. However, when there is little or no surface residue, timely shallow tillage following significant rainfall events may be useful to ensure that enough seedzone soil water will be present after late summer drought periods to effect seed germination and stand establishment of winter wheat. Tillage to depths of 8 to 15 cm is not desirable because the soil will dry out to the depth of tillage, which negates the possibility of obtaining a stand of winter wheat unless sufficient rainfall occurs to rewet the tilled layer. Regardless of the advantages or disadvantages of tillage at a given time, the amount of crop residue produced is the key factor in determining need for tillage.

To fulfill the objectives of managing the soil to maximize water conservation and seedzone soil water, and to minimize or eliminate wind and water erosion, management guidelines must be rather site specific and compatible with the specific soil-site characteristics and the quantity of crop residue present at the time a management decision is made. For example, during non-crop or fallow periods, irrational use of certain tillage implements such as the plow or disk, that destroy or bury most crop residue, usually necessitates additional tillage. Soil aggregate deterioration by normal weathering processes is enhanced on bare, unprotected soil, compared with soil protected by crop residue. Thus, a given sequence of tillage operatiions can become somewhat counterproductive to soil improvement and protection, and with time may further intensify soil degradation.

Minimum-tillage and no-till cropping systems that maintain crop residues on the land increase dry aggregate size and stability, reduce wind and water erosion, and increase soil water storage. Even when crop residue levels at harvest are low (< 2000 kg ha^{-1}), protecting soil from erosion should be the primary concern. Tillage should be eliminated, if possible, or reduced to that required only to ensure seedzone soil water concentrations sufficient for establishing a wheat crop. When crop residue

levels at harvest range between 2000 and 4000 kg ha $^{-1}$, selections should be made among no-till, no-till and reduced tillage, or reduced tillage systems best suited to the soil and climatic constraints of the area. Management of large amounts of wheat straw ($>$ 4000 kg ha $^{-1}$) causes some difficulty in preparing a seedbed for the next crop, particularly if most of the residue is lying on the soil surface and the period between crops is relatively short, as with annual cropping. Optimum quantity and height of stubble remaining in the field can be controlled by carefully selecting crop cultivars, adjusting the combine platform cutting height, and chopping, bunching, or baling a selected amount of straw for removal from the field. The development and acceptance of semidwarf cultivars of spring wheat has made recropping and no-till seeding of winter wheat feasible (Black and Siddoway, 1977b; Halvorson et al., 1976).

Because of all the subsequent beneficial effects crop residues have on reducing soil erosion and improving soil properties, limited tillage and no-till cropping systems become cumulatively more beneficial with time, thereby improving the physical, chemical, and biological properties of dryland soils. Long-term benefits of conservation tillage systems, as opposed to more intensive tillage systems (conventional tillage), have been documented. Bauer and Black (1981) reported that organic soil C was 44 and 13% and soil N was 34 and 10% higher for coarse- and moderately fine-textured soils, respectively, after 25 yrs of stubble mulch fallow (herbicide plus wide blade sweep) than adjacent soils on the same series tilled conventionally. These differences were attributed to the superior soil erosion protection afforded by stubble mulching and not to differential fertilizer practices or residue production. Unger (1968) also showed higher organic matter and soil N levels after 24 yr with reduced tillage than one-way disk for wheat-fallow and continuous wheat cropping systems. The adoption of conservation tillage and no-till systems of crop production is a recognition of the importance of maintaining adequate crop residue during noncrop periods with or without summer fallow and during crop establishment, to minimize soil loss by wind and water erosion. The sustained success of dryland agriculture depends upon a unique blend of agricultural sciences, all based on the underlying principle of conserving the soil while using available water efficiently.

6C Soil Reaction—Acidity, Alkalinity, and Salinity

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6C–1 ACIDITY

Wheat, *Triticum aestivum (L.)*, unlike legumes, has a relatively high tolerance to soil acidity. Good forage growth and grain production can be obtained with soil pH as low as 5.0 to 5.2 (Westerman, 1981). However, lime recommendations based on soil buffer index values are normally made when the soil pH drops below 5.5 to ensure a margin of safety (Johnson and Tucker, 1982).

The adverse effects of soil acidity on plant growth and the benefits due to liming have been well documented over the years (Blair and Prince, 1923; Fried and Peech, 1946; Wright, 1948; Schmehl et al., 1950; Foy and Brown, 1964; Evans and Kamprath, 1970; White, 1970; Hutchinson and Hunter, 1970; Westerman, 1981).

Aluminum toxicity is probably the most detrimental factor affecting plant growth when the soil pH drops below 5.5. Marion et al. (1976) described the relationship between pH and the distribution and average charge of soluble Al species. Due to the amphoteric nature of Al, at pH 5.5 the predominant species is $Al(OH)_2^+$ at pH 5.5, whereas below pH 4.7 the predominant species is Al^{+3}. At pH values of 5.0 and below, excess Al accumulates in the soil solution and reduces root growth, respiration, and DNA synthesis; reacts with other nutrients such as P to form less available compounds; interferes with the uptake and transport of other elements in plants such as Ca, Mg, P, K, and water; and inhibits growth of microorganisms necessary for nitrification in soil (Foy et al., 1978; Wallace and Anderson, 1984). Plants suffering from Al toxicity are often susceptible to drought because roots are shortened and stubby, with fine branching.

Manganese also becomes more soluble in soil solution as pH de-

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creases (White, 1970). Manganese toxicity is enhanced when soils are waterlogged even for short periods of time, which allows the reduction of Mn^{4+} and Mn^{3+} to Mn^{2+}. Unlike Al, Mn toxicity symptoms are more noticeable in plant tops than in roots. Generally, marginal leaf chlorosis and necrotic spots on leaves are observed with excess Mn concentrations in the soil solution. Both Al and Mn toxicities may occur simultaneously; however, Al toxicity is generally considered to be more detrimental (Foy et al., 1978).

Since both Al and Mn solubilities decrease with increasing soil pH, liming soil to a pH of 5.5 or greater is an easy correction. If lime is unavailable and Al toxicity is a problem, a different cultivar may be the answer. There is considerable tolerance in different wheat cultivars to Al toxicity (Foy et al., 1965; Fleming and Foy, 1969; Foy et al., 1974; Lafever et al. 1977; Mugwira et al., 1981; Unruh and Whitney, 1984). However, since the efficiency and uptake of other essential nutrients also are reduced under acidic conditions, liming remains the most desirable solution for correction of both Al and Mn toxicities.

Many factors contribute to soil acidification in wheat production systems (Westerman, 1981). High yields of good quality wheat forage and grain require adequate fertilization with essential plant nutrients. The relative acidity and basicity of fertilizer sources have been discussed by Pierre (1933) and Andrews (1954). Nitrogen is generally the element required in the largest amount. Soil test calibrations at Oklahoma State University (Johnson and Tucker, 1982) indicate that approximately 33 kg N Mg^{-1} (2 lb N/bu) is required for grain yield goals up to 3360 kg ha^{-1} (50 bu/Ac) and an additional 30 kg N Mg^{-1} (60 lb N/ton) of dry matter forage removed by pasturing. The N must be in the soil or supplied as fertilizer. Regardless of the source of ammoniacal N, all ammoniacal N forms will produce acidity (H^+ ions) via the natural nitrification process in soils as indicated below:

$$2NH_4^+ + 3O_2 \xrightarrow{\text{Nitrosomonas spp.}} 2HO_2^- + 4H^+ + 2H_2O$$

$$2NO_2^- + O_2 \xrightarrow{\text{Nitrobacter spp.}} 2NH_3^-$$

The acidification effect of fertilizers is not always detrimental. Many soils in the Great Plains are alkaline with a high buffer capacity and the acidity that is produced is beneficial. In other cases where soil pH values are low ($pH \leq 5.5$), the potential for reduction in yields exists with continued use of acid-forming fertilizers unless corrective lime applications are made.

Basic cation removal (Ca, Mg, K, and Na) in wheat forage, grain, and straw is also a contributing factor to soil acidity. More specifically, the Excess Base/N ratio (EB/N) (Pierre et al., 1973; Pierre and Banwart, 1970) can be used to estimate the contribution of crop production to soil acidity. Excess base, as the term implies, represents the excess of base-forming over acid-forming elements in plants or plant parts. Thus, EB/

N is defined as the total cations minus the total anions divided by total N expressed as meq 100 g^{-1} of plant material:

$$EB/N = (Ca^{2+} + Mg^{2+} + K^{+} + Na^{+}) - (Cl^{-} + SO_4^{2-} + S + H_2PO_4^{-} + NO_3^{-}\text{-N})/\text{total N}.$$

An EB/N ratio less than one would decrease the acidity produced by nitrification of NH_4^+ to NO_3^- and an EB/N ratio greater than one would increase it. In winter wheat production, forage removal by grazing and removal of grain at harvest will reduce the amount of lime required for neutralization of the acidity produced by ammoniacal fertilizer, whereas removal of straw will increase the lime requirement (Table 6C–1). Both forage and grain have EB/N ratios < 1 (approximately 0.4 and 0.04, respectively), whereas the EB/N ratio of wheat straw is 1.2. In the case of forage and grain removal, considerable N is also removed, leaving behind basic residues of Ca, Mg, K, and Na in soil that neutralize the acidity produced by nitrification of ammoniacal N. Removal of straw depletes the bases in soil faster than the N and further enhances the acidification of ammoniacal N. The theoretical potential acidity from N fertilization was shown to be reduced 77 and 97%, respectively, due to grazing and grain removal (Westerman, 1981). Straw removal without grain or forage removal would increase the theoretical acidity produced by ammoniacal N fertilization 120%. In combined practices that involve grazing and grain removal, grain and straw removal, and grazing, grain, and straw removal, the theoretical potential acidity would be reduced 87, 64, and 70%, respectively. The effect of straw removal after harvest becomes apparent. Excess base/N ratios of crop species, as well as plant parts within species, vary and affect acidity produced by N fertilization accordingly.

Decomposition of wheat residue in soil also results in soil acidification. Carbon dioxide is released from organic residues during decomposition and combines with water to form carbonic acid (H_2CO_3). Carbonic acid dissociates into H^+ and HCO_3^-, resulting in another source of H^+ for increasing soil acidity. Root activity and metabolism may also serve as a source of CO_2.

Leaching of exchangeable bases (Ca^{2+}, Mg^{2+}, K^+, and Na^+) out of the effective root zone is also a contributing factor to increased soil acidity. Hydrogen and/or Al^{+3} generally replaces these basic cations when they are leached, which enhances the soil acidification problem. This problem is more pronounced in sandy soils under high rainfall or irrigation than in clay or clay loam soils.

6C–2 ALKALINITY

Problems associated with alkalinity in wheat production are twofold: decreased water infiltration, and decreased availability of micronutrients.

Table 6C–1. Effect of winter wheat production on the theoretical potential acidity resulting from the application of ammoniacal N. Source: Westerman, 1981.

Fertilizer and crop removal system	Yield of dry matter	N removed	Excess† base removed	N	EB	EB/N	100% ECCE Lime required for Neutralization	Theoretical potential acidity
	kg ha^{-1}			meq 100 g^{-1}			kg ha^{-1}	%
224 kg N ha^{-1} × fallow	---	---	---	---	---	---	403	100
224 kg N ha^{-1} + grazing‡	2 240	90	73	286	66	0.23	92	23
224 kg N ha^{-1} + grain	4 032	81	11	143	5	0.03	12	3
224 kg N ha^{-1} + straw	4 480	31	132	50	60	1.20	484	120
224 kg N ha^{-1} + grazing + grain	6 272	170	84	194	25	0.13	53	13
224 kg N ha^{-1} + grain + straw	8 512	112	143	94	33	0.36	146	36
224 kg N ha^{-1} + grazing + grain + straw	10 752	202	216	134	40	0.30	121	30

†Excess base (EB) expressed as $CaCO_3$.
‡Calculations for grazing are for removal and do not include basic cations and N returned to the soil in manure.

The solubilities of Fe, Mn, Cu, and Zn decrease markedly with increased soil pH. Iron chlorosis symptoms may occur in winter wheat production systems when the soil pH exceeds 8.0. The configuration of Fe chlorotic areas in fields are irregular in shape and generally occur in severely eroded areas and/or areas that have been leveled for irrigation and have low amounts of organic matter in the surface. Zinc, Cu, and Mn deficiencies due to alkalinity are not a severe problem in most of the major wheat producing areas; however, Mn deficiencies have been reported in the southeastern USA (Fales and Ohki, 1982; Ohki, 1984).

6C-3 SALINITY

Water infiltration is decreased in alkaline soils due to the blockage of soil pores by dispersed clay and organic matter colloids. Hence, wheat production may be reduced as a result of physiological drought even when surface soil moisture is excessive in these areas. Exchangeable Na percentage > 15 is used to identify this condition; improved internal drainage and the addition of organic matter and gypsum are helpful in reclamation.

The accumulation of soluble salts in the soil profile can have a detrimental effect on plant growth. Different crops have different tolerances to salinity. Wheat is generally considered to have moderate tolerance to salinity, but is more sensitive than cotton (*Gossypium hirsutum* L.), grain sorghum [*Sorghum bicolor* (L.) Moench], and barley (*Hordeum vulgare* L.) (U.S. Salinity Laboratory Staff, 1954). Most plants are particularly susceptible during germination and in the seedling stage. The overall effect of salinity is reduced plant growth and yield. Salt problems in soils and their effect on plant growth can be subdivided into four categories, namely, normal, saline, saline-sodic, and sodic.

Reclamation and amelioration is specific to each problem, and it is extremely important to identify and characterize the problem before corrective soil amendments and management practices are applied. Excessive salt can be reduced by leaching. Poor internal drainage is usually the cause of salt accumulation and often it is necessary to improve drainage by installing tile drains. Amendments such as gypsum ($CaSO_4 \cdot 2H_2O$) and organic matter are beneficial in providing a more porous surface to increase infiltration and leaching, particularly when soils have excess Na. Reclamation of salt-affected soils is a slow process and several years may be required for correction.

6D Nutrient Requirements and Fertilizer Use

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After a century of extensive rather than intensive efforts in wheat production in North America, researchers and growers have begun to implement improved management to achieve higher yields. Fertilizer management is an important part of the overall management package aimed toward higher yields. Higher wheat yields per hectare are an important tool in combatting increasing costs per unit of production.

It is important to recognize that production costs per hectare may rise with improved management inputs, including the use of larger amounts of supplemental nutrients; however, production cost per unit yield generally declines as yields increase. This is the real focus of improved management: lower production costs per unit and higher profitability. Admittedly, one can apply so much of an input that costs outstrip returns, but basically the fact remains that as yields go up, production costs per unit drop and profits increase.

High yields require large amounts of nutrients. Washington data (Table 6D–1) indicate the amounts of nutrients that accumulate in the aboveground portions of a wheat crop yielding 7.3 Mg ha^{-1}. Actually, estimates for the amount of N needed for a complete crop (roots, vegetative portion, and grain) range from 30 to 50 kg N per Mg of grain (Tables 6D–2,3). It is important to remember that both soil nutrients and fertilizer-supplied nutrients can meet these needs, and farmers must consider inputs from all sources.

As nutrient rates increase to meet higher yield goals, the importance

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Table 6D–1. Nutrient uptake of wheat by growth stage—7.3 Mg ha^{-1} yield in Washington. Source: Koehler, 1985.

Nutrient	Growth stage				Total accumulation for season
	Tillering (0–30 days)	Boot (31–73 days)	Milk (74–93 days)	Mature† (94–114 days)	
	kg ha^{-1}				
N	42	78	56	−19	176
P	7	23	17	− 3	47
K	18	100	15	−36	133
S	1	7	3	0	11
Dry matter	885	6 238	5 029	2 005	14 157
	Percent of maximum uptake				
N	24%	68%	100%	89%	
P	15	65	100	94	
K	14	89	100	73	
S	10	60	100	100	
Dry matter	6	50	86	100	

†Shows net loss of N, P, and K due to leaf drop.

Table 6D–2. Total N requirements (soil + fertilizer) for optimum wheat production in the Great Plains and Pacific Northwest.

Location	System†	Wheat type‡	kg N Mg^{-1} grain	Reference
Saskatchewan	D	HRS	42	Campbell et al., 1984
North Dakota	D	HRS	40	Dahnke and Swenson, 1983
North Dakota	D	HRS	40	Goos, 1983
Montana	D	HRS	33	Black and Ford, 1976
Montana	D	HRW	40	Halvorson et al., 1976
Montana	I	HRS	37	Christensen and Killorn, 1981
South Dakota	D	HRS&W	40	Adams et al., 1978
South Dakota	D	HRS&W	40	Gelderman et al., 1977
Idaho	I	SWW	33	Brown, 1982
Idaho	D	SWW	45	McDole et al., 1978
Oregon	D	HRW§	38–43	Gardner and Goetze, 1980
Oregon	D	SWW§	38–43	Gardner and Goetze, 1980
Oregon	D	HRS¶	28–33	Gardner and Goetze, 1980
Oregon	D	SWW¶	28–33	Gardner and Goetze, 1980
Oregon	I	SWW	42–50	Gardner et al., 1983
Washington	I	HRS	40	Sanmaneechai et al., 1984

†D = Dryland and I = Irrigated.
‡HRS = Hard Red Spring, HRW = Hard Red Winter, and SWW = Soft White Wheat.
§Tall cultivars.
¶Semidwarf cultivars.

of a complete management package becomes even more pronounced. More complete attention to pest control and possible use of plant growth

Table 6D–3. Total estimated N requirements (soil + fertilizer) for optimum wheat production in the central Great Plains, Southwest, and West.

Location	Crop	kg N Mg^{-1} grain	Reference
Kansas	Hard red winter	33 to 40	Whitney, 1979
Oklahoma	Hard red winter	37 to 40	Johnson and Tucker, 1984
Texas	Hard red winter	33	Ashlock, personal communication, 1984†
			Welch et al., 1981
Missouri	Soft red winter	33	Buchholz, 1983
Colorado	Hard red winter	33 to 41	Westfall, personal communication, 1984‡

†Lanny Ashlock, Dep. of Agronomy, Texas A&M University, College Station.
‡D. G. Westfall, Dep. of Agronomy, Colorado State University, Ft. Collins.

regulators, as well as selection of the proper hybrids and cultivars, becomes increasingly important.

6D–1 FERTILIZING WHEAT IN SEMIARID REGIONS

Good farm management practices are essential for optimum yield responses of wheat, *Triticum aestivum* (L.), to fertilization. These practices include: (i) proper irrigation management; (ii) water conservation for dryland farming; (iii) use of high-yielding cultivars; (iv) use of soils suitable for wheat production; (v) adequate weed control; (vi) disease and insect control; (vii) appropriate crop residue management practices; (viii) proper seeding methods and equipment; (ix) crop rotations; and (x) timely harvest operations. The four nutrients of major concern to wheat producers in the northern Great Plains and Pacific Northwest are N, P, K, and S.

Soil analysis is a first guide to efficient fertilization. Nitrogen is mobile in the soil and is subject to leaching and denitrification losses. The level of N in the soil can also increase temporarily through mineralization. Thus, a soil test for residual N (NO_3^- or NO_3^- and NH_4^+) is recommended each crop year as a guide for making fertilizer recommendations. Phosphorus and K, in contrast, are relatively immobile in the soil and are lost from the root zone mainly by crop removal and erosion. Soil tests for P and K each crop year are not essential, but are recommended to monitor changes resulting from fertilization and crop removal. Soil tests for S are not as effective as those for N, P, or K, but when used with past cropping history, yield goals, and plant tissue analysis for S, help predict the need for S fertilization in wheat.

6D–1.1 Nitrogen Management

6D–1.1.1 Soil Testing

Soil testing for residual NO_3^--N requires that soil samples be collected to a depth of at least 60 cm to estimate the level of plant-available N.

Sampling to greater depths (120 to 150 cm) is recommended to improve the accuracy of the N recommendations. Residual soil NO_3^--N can be influenced by previous crop, previous level of N fertilization, quantity of crop residue returned to the soil, length of summer-fallow period, quantity of soil organic matter, climate, cropping sequence (e.g., crop–fallow vs. annual cropping), and other factors. Therefore, a soil test for NO_3^--N is essential to accurately estimate fertilizer N needs.

There is some variation between laboratories in terms of how the residual NO_3^--N values are used in making recommendations. Most consider the residual NO_3^--N in the surface 60 to 120 cm of soil to be 100% available and merely subtract that amount from the N fertilizer recommended for the particular yield goal.

Basically, soil organic matter in the semiarid regions of North America is less able to supply sufficient N through mineralization for adequate yields of wheat than was the case in the early 1970s. Organic matter in soils has declined with tillage and in many areas is low enough that supplemental N is now required to allow new hybrids and cultivars to express yield potentials. Fewer soil testing labs are including organic matter in their N availability estimates.

6D–1.1.2 Choosing Yield Goals

Estimating N fertilizer needs of nonirrigated spring and winter wheat requires an accurate estimate of protential grain yield. Estimating potential grain yield requires consideration of both the amount of soil water at planting and the expected growing season precipitation. The amount of soil water present is influenced by soil texture, climate, effective rooting depth of the crop, crop rotation, tillage system, and cropping system. Balancing N requirements with available water and yield potential is essential to ensure economic returns. Water is the factor most often limiting dryland wheat yields in the semiarid regions. Therefore, wheat yield estimates often reflect the quantity of water expected to be available to the crop (Bauer et al., 1967; Halvorson and Kresge, 1982; Jackson et al., 1983a; Leggett, 1959; McDole et al., 1978; Leholm and Vasey, 1983).

Dahnke et al. (1983) state that choosing a yield goal is one of the most important decisions farmers make. Since fixed costs per hectare are the same with low or high yields, profits in relation to fixed costs increase as yields increase. Variable costs, including N, increase as potential yields increase. Choosing a realistic yield goal helps ensure that returns from variable costs such as N are greater than input costs.

A yield goal is a target; yields hoped for and those actually obtained are a function of both controllable and uncontrollable factors. Management, including choice of rates of fertilizer, is a controllable factor, one of the things that helps to lower crop production risks. However, if decisions on inputs are viewed with the philosophy that, since the yield goal might not be obtained, nothing can be risked, then that is a conscious decision for a poor yield goal and poor profits.

Dahnke et al. (1983) point out that a realistic yield goal which will determine the amount of N to apply for wheat can vary all the way from past yield levels to the maximum potential for a given area. Maximum potential yields are probably too high to be practical goals. On the other hand, average yield is a goal that is too low. If N or any other applied nutrient is adequate only for an average yield, the maximum yield obtained would be the same as the past average yield and the average yield in the future would actually drop, since the old average has been set as the new maximum.

Dahnke et al. (1983) suggest that a practical range for a yield goal should be somewhere between above average to the highest yield that has been obtained in the area under similar conditions. Obviously, a number of factors can affect the yield goal, including availability of capital to spend on fertilizer. But for a sound financial approach to wheat production, the yield goal should probably be close to the maximum yield obtained in the area.

Dahnke et al. (1983) point out that the key reason for fertilizing for maximum yields is that unused nutrients carry over. That is, when sufficient nutrients are applied for a specific yield but that yield goal is not reached because of poor growing season conditions, the nutrients will carry over and be available for future crops. In this case, the added cost to the grower is the cost for one year's interest on the money used to purchase nutrients that were not used in the year of application. That could amount to \$1.25 to \$2.50 ha $^{-1}$ if the yield goal for wheat was 600 kg ha $^{-1}$ above actual yield. But on the other hand, if the yield goal was 600 kg ha $^{-1}$ low, the unrealized yield would be worth \$66 ha^{-1} when wheat was worth \$110 Mg $^{-1}$. For example, it costs about \$12 ha $^{-1}$ for enough extra N (at 37¢ kg $^{-1}$) and P (at 62¢ kg $^{-1}$ of P_2O_5) to supply nutrients for an added 600 kg ha^{-1} of wheat. With wheat at \$110 Mg^{-1}, that is more than a 5:1 return on dollars invested.

6D-1.1.3 Estimating N Requirements

Based on the potential yield estimate, the total N requirement is calculated by multiplying the estimated yield by the N required per unit of grain yield. The residual soil NO_3^--N to a depth of 60 to 150 cm of soil is subtracted from this value. The result is the estimated fertilizer N requirement. The quantity of N (soil + fertilizer) recommended to optimize wheat yields varies from 33 to 50 kg N Mg^{-1} grain, depending upon geographic area and water supply with 40 kg N Mg^{-1} grain being about average in the northern Great Plains (Table 6D–2) and 33 to 40 kg N Mg^{-1} grain about average for the central and southern Great Plains (Table 6D–3). Maximum yields may require slightly more N to produce a unit of grain and maintain quality because of decreased N-use efficiency with increasing yield level.

Adjustments to the fertilizer N recommendation are needed if: (i) large quantities of mineralizable N are expected; (ii) large quantities of

crop residue were returned to the soil; (iii) the previous crop was a legume; (iv) manure was applied; and/or (v) a reduced-tillage or no-till cropping system is being initiated. Check the recommended adjustments to the N fertilizer recommendation for your area. For example, if the previous crop was a legume, the rate of N fertilizer recommended could be reduced 25 to 50 kg N ha $^{-1}$, depending on the geographic area (Dahnke and Swenson, 1983; Brown, 1982).

Credits for residual N from legumes vary, ranging from 0 to as high as 120 or 140 kg N ha^{-1}. Oplinger and Wiersma (1984) have reported a formula for calculating legume N contributions:

$$40 \text{ kg} + (1 \text{ kg} \times \% \text{ legume in the stand}) = \text{N available 1st yr.}$$

Kansas recommendations (Whitney, 1979) do not give credit to legume stands of $< 50\%$ but suggest a credit of 120 to 150 kg N ha^{-1} the 1st yr after an excellent legume stand is destroyed. The 2nd yr after the legume, 50% of the original N credits will provide an estimate of N released to a crop.

Soybean [*Glycine max* (L.) Merr.] also provides some carryover N for wheat. Although the amounts are difficult to document, many recommendations call for a credit of 1 kg of N per 60 kg of soybean yield.

Although manure disposal on wheat land is not common in arid or semiarid regions, N from manure should be included in calculations of amounts available to the crop. Manure composition varies widely, ranging from 1 to 3% total N on a dry matter basis, depending upon how the manure has been handled (Wallingford et al., 1975; Powers et al., 1975). The most precise way of estimating N availability is to have a manure analysis. If that is not available and if the manure has been stockpiled outside, assume 0.8 to 1.25% N. Also assume about 50% N availability the 1st yr from the manure. As an example, an application of 10 Mg manure per ha at 10 g N per kg manure with 50% availability the 1st yr would provide 50 kg N ha $^{-1}$. The 2nd yr, about another 25% of the original amount (25 kg) of N would become available (Powers et al., 1975).

Fertilizer N rates should be increased by 10 to 20 kg N ha $^{-1}$ for each Mg ha $^{-1}$ of small grain straw or maize residue returned to the soil from the previous crop. Placing the N fertilizer in a concentrated band on or below the soil surface may reduce the immobilization of N by microbes and reduce the amount of additional fertilizer N needed, particularly in reduced tillage and no-till systems. If the previous crop residues were removed or the field is fallowed between crops, no additional fertilizer N is recommended.

Grazing wheat is a practice common to the central Great Plains and Southwest. Forage removal places additional stress on N supplies and should be considered in compiling N recommendations. Oklahoma guidelines (Johnston et al., 1983; Johnson and Tucker, 1984) suggest

calculating additional N needs based on 10 kg of dry forage per kg of animal gain and assuming a N concentration of 30 g N kg $^{-1}$ forage. Research conducted by the Noble Foundation indicates forage yields from December to 1 March of 1200 to 2000 Kg ha $^{-1}$ of dry matter, with average daily rates of gain by stocker cattle at 0.7 to 0.8 kg per head (J. Rogers et al., The Noble Foundation, Box 2180, Ardmore, OK 73401, 1985 personal communication). Assuming a value of 1500 kg of forage removed per ha and containing 30 g N kg $^{-1}$, an additional 45 kg N ha^{-1} would be required to provide sufficient N for the targeted yield goal. Kansas recommendations call for an additional 17 to 34 kg N ha^{-1} if wheat is heavily grazed. On a gain basis, about 1 kg of N will be required to replace that removed in 3 kg of animal gain.

In summary, N fertilizer requirements for wheat can be estimated in the following manner.

Example for Estimating N Fertilizer Needs of Wheat

A. Total N required = yield goal (Mg ha $^{-1}$) × N requirement (kg N Mg $^{-1}$ grain).

B. Add N required for residue decomposition (wheat, maize, grain sorghum), 20 kg N^{-1} Mg^{-1} per ha.

C. Add N to replace that removed in grazing, 1 kg N ha^{-1} per 3 kg of gain.

D. Subtract residual soil NO_3^--N and/or NH_4^+-N, kg N ha $^{-1}$ to a depth of 120 cm.

E. Subtract any N credit reported for organic matter mineralization, kg N ha $^{-1}$.

F. Subtract residual N from alfalfa, amount dependent upon legume stand, kg N ha $^{-1}$.

G. Subtract residual N credit for soybeans, 1 kg N per 60 kg beans; other beans, 35 to 50 kg N ha^{-1}.

Total N required = A + B + C − D − E − F − G.

More fertilizer N is required each crop year with annual cropping systems than with a crop-fallow system (Alberta Agriculture, 1981; Black and Siddoway, 1977b; Halvorson et al., 1976; Halvorson and Black, 1985a; Sanmaneechai et al., 1984). The N requirements of irrigated hard red wheat per unit of yield are similar to those for dryland (Table 6D–2).

The high-yielding soft winter wheats grown in the Pacific Northwest have a low protein content, which is desirable for maintaining good baking qualities for pastries. Large increases in grain yield are common in the Pacific Northwest due to N fertilization (Gardner and Nibler, 1984). Brown (1982) reported a total N requirement for these irrigated soft winter wheats of 33 kg N Mg $^{-1}$ of grain yield. Overfertilization of the soft winter wheats with N may increase grain protein above 10%, resulting in reduced milling performance and baking quality of the wheat (Harder and Thiessen, 1971; Johnson et al., 1984).

6D–1.1.4 Nitrogen Sources

Major N sources used in the semiarid regions are anhydrous NH_3, urea-ammonium nitrate solution (UAN), $(NH_2)_2CO$ (urea), NH_4NO_3, and $(NH_4)_2SO_4$. Anhydrous NH_3 for direct application has been the dominant N source in the area for years.

In recent years, the use of both UAN and urea has grown, while NH_4NO_3 use has declined. Adaptability of UAN for combined applications of pesticides and fertilizer has been a significant factor in increased use. The relatively low cost of urea, combined with increased production capability for that material, has significantly affected its use compared to other solid N sources.

Type of N fertilizer used for wheat does not influence N-use efficiency if the material is applied to minimize NH_3 losses and germination problems are prevented (Gibson et al., 1980; Pumphrey and Rasmussen, 1982). Direct seed application of urea can lead to detrimental effects on plants. Urea in the soil rapidly hydrolyzes, producing some free ammonia. The presence of free NH_3 close to or in direct seed contact can lead to germination damage, particularly on high pH soils. Montana data cited by Smith et al. (1973) demonstrated that urea N applications in direct seed contact can cause germination damage. Kelley et al. (1977) also noted detrimental effects from urea-containing products such as urea ammonium phosphate (UAP) placed in direct contact with wheat seed even on slightly acid soils (Table 6D–4).

Rates of N fertilizers such as urea which contain or produce NH_4^+ and NH_3 should not exceed 11 to 20 kg N ha^{-1} if placed in seed contact in narrow (3 cm) bands, particularly on the calcareous (soils) dominant in the central and northern Great Plains (Alberta Agriculture, 1981; Black et al., 1980; Pairintra, 1973; University of Saskatchewan, 1981). Lower rates of N with the seed should be used on sandy soils, when soil moisture conditions at seeding are poor, or when soil pH is above 7.3. When seed is distributed in wide bands, such as those made with some air-seeders, higher rates (up to 40 kg N ha^{-1}) of urea can be used without a loss in yield (Deibert et al., 1985). Anhydrous NH_3 has been applied at a depth of 10 to 15 cm, less than 24 h prior to seeding spring wheat, without detrimental effects on grain yield (Varvel, 1982; A.D. Halvorson, unpublished data, USDA–ARS, Akron, CO). The important point is not to place pre-plant NH_3 and seed in the same soil zone.

Table 6D–4. Phosphorus sources have shown comparable effects on wheat in Kansas. However, urea phosphate placed in direct seed contact can lower yields. Source: Kelley et al., 1977.

Treatments	1976	1977
	Mg ha^{-1}	
Control, No P	1.48	1.88
Urea phosphate (UAP)	2.22	2.35
Ammonium polyphosphate (APP)	2.28	2.69
Diammonium phosphate (DAP)	2.28	2.69
$LSD_{0.05}$ Carrier	NS	0.27
P Broadcast	2.28	2.28
P Banded (direct seed contact)	2.28	2.82
$LSD_{0.05}$ Method	NS	0.40

N rate: 87 Kg N ha^{-1}.
Mean P application, 24 kg P ha^{-1}. Low P soil test. Soil pH 5.5.

Urea has occasionally been less effective than NH_4NO_3 as a source of N in the northern Great Plains, particularly when used in broadcast applications not incorporated into the soil (Black and Siddoway, 1971; Christensen and Meints, 1982; Campbell et al., 1984). Placing urea in a concentrated band below the seed can correct these lower utilization efficiencies (Robertson, 1982; Tomar and Soper, 1981).

Kissel (1982) noted that a survey of results across the central Great Plains area indicated that generally there were few differences in wheat growth or yield that could be attributed to the source of N used. He noted the potential for losses of N by volatilization of NH_3 from urea and UAN, but also pointed out that actual losses must be extremely limited in view of comparatively equal performance of N sources when topdressed on wheat. He suggested that low temperatures at normal topdressing time (January–March) tended to negate any potential for volatilization losses to occur. Obviously, this type of general statement of comparable performance of N sources assumes that proper application methods are involved.

Some evidence of the comparable performance of various N sources for wheat in the central Great Plains and Southwest is provided in Tables 6D–5 and 6. Pre-plant N applications of anhydrous NH_3, urea, and NH_4NO_3 performed in an equal manner when averaged across a large number of locations. Topdressed applications of various N sources were also comparable.

Some conditions do exist which might favor choice of one N source over another. Reduced-tillage or no-till conditions, which tend to leave very large amounts of residue on the soil surface, could be conducive to poorer performance of urea or urea-containing material such as UAN. Poor soil contact could contribute to NH_3 volatilization losses. Schneider et al. (1978) reported lower efficiency of urea compared to NH_4NO_3 for no-till wheat in western North Dakota (Table 6D–7). However, these differences occurred with broadcast, unincorporated applications of N and lesser differences would be expected if N were placed below the residue or concentrated in surface band or dribble applications (Fig. 6D–1).

Kissel (1982) pointed out that N source comparisons for wheat have also been carried out on high pH calcareous soils, without substantial

Table 6D–5. Comparisons of N carriers for wheat in Kansas have shown few consistent differences. Source: Murphy, L. S., Kansas Fertilizer Handbook—1969, p. 38.

	Anhydrous ammonia		Ammonium nitrate		Urea	
N rate	Yield	Protein	Yield	Protein	Yield	Protein
kg ha^{-1}	Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	g kg^{-1}
0	1.75	116	1.75	117	1.75	117
28	2.08	122	2.08	120	2.08	120
56	2.15	123	2.15	124	2.28	126
84	2.35	132	2.28	129	2.28	130
112	2.28	134	2.28	130	2.22	136

Table 6D–6. Nitrogen sources have usually shown comparable efficiency under topdressed conditions for wheat in Kansas. Sources: Gallagher et al., 1973a; Harms et al., 1974; Gallagher et al., 1975.

Nitrogen source†	Harvey Co.	Stafford Co.	Riley Co.	Reno Co.	McPherson Co.	Harvey Co.	Brown Co.
	Mg ha^{-1}						
Control	1.91	2.63	2.17	1.94	1.01	1.88	3.04
Urea	3.42	3.59	2.62	3.18	1.95	2.42	4.45
Ammonium nitrate	3.21	3.76	2.56	—	1.68	2.28	4.33
UAN‡	—	—	—	3.33	1.88	2.49	4.37
Soil pH	5.4	5.4	6.2	6.0	5.8	6.4	6.2
Soil texture	Loamy fine sand	Loamy fine sand	Silt loam	Silt loam	Silt loam	Loamy fine sand	Silty clay loam

†Mean N rate all locations: 67 kg N ha^{-1}.
‡UAN = urea–ammonium nitrate solution.

Table 6D–7. Responses of no-till spring wheat to ammonium nitrate and urea in North Dakota. Source: Schneider et al., 1978. Olaf spring wheat.

N rate	Nitrogen source	Yield	Protein	Water-use efficiency
kg ha^{-1}		Mg ha^{-1}	(g kg^{-1})	(kg ha^{-1} per cm)
0		1.15	149	33.9
20	Ammonium nitrate	1.61	145	51.0
20	Urea	1.86	142	53.9
40	Ammonium nitrate	1.92	144	63.7
40	Urea	2.06	141	62.3
60	Ammonium nitrate	2.55	142	74.4
60	Urea	1.82	147	57.4
80	Ammonium nitrate	2.54	146	72.1
80	Urea	1.58	159	46.6
100	Ammonium nitrate	2.52	150	73.0
100	Urea	1.70	161	52.3
$LSD_{0.05}$		0.30	3	9.7

Fig. 6D–1. Dribble or surface band application of fluid or solid fertilizers produces a concentrated zone of nutrients in the soil even when tillage follows the application. Dribble application of fluid fertilizers allows use of conventional equipment with relatively simple modifications. Courtesy: Ag Chem Equip. Co.

differences between N sources. An exception would be the performance of $(NH_4)_2SO_4$ on calcareous soils. Texas studies (Hargrove et al., 1977) indicated that NH_3 loss from $(NH_4)_2SO_4$ can be substantial when high temperatures (30 °C) occur at the time of fertilization. Direct comparisons of NH_3 losses from various N sources (Table 6D–8) indicated that volatilization losses from $(NH_4)_2SO_4$ ran as high as 23% of the applied N in 15 days after application, but losses from NH_4NO_3 urea, and UAN (32% N) were only 5%, 1.5%, and 1.5%, respectively. Based on these and other studies, Kissel (1982) concluded that the potential for NH_3 volatilization losses from urea or urea-containing fertilizers on high pH soils is no greater, in fact probably is less, than for $(NH_4)_2SO_4$, NH_4NO_3, and $(NH_4)_2HPO_4$. Ammonia losses from noncalcareous soils (pH $<$ 7.3) are not likely. However, differences in environmental conditions, including high temperature, heavy dew, and small amounts of precipitation, will

Table 6D–8. Volatilization loss of NH_3 during 15 days after topdress applications of four N^1 sources on wheat in Blackland Research Center, Temple, TX. Source: Kissel, 1982.

	Nitrogen source			
	Ammonium nitrate	Ammonium sulfate	Urea	UAN
	N loss			
Nitrogen loss, kg ha^{-1}	2.8	13.1	0.84	0.84
Percent of applied	5.0	23.4	1.5	1.5

N rate: 56 kg N ha^{-1}

Table 6D–9. Deep-placed pre-plant UAN solution was more effective for winter wheat than broadcast N. Stafford County, KS. Source: Gallagher et al., 1976.

N rates	Method of N application	Time of N application	Grain yield	Grain protein
kg ha^{-1}			Mg ha^{-1}	g kg^{-1}
0	—	—	1.94	107
33	Deep placed	8 July	1.99	108
67	Deep placed	8 July	2.80	109
100	Deep placed	8 July	3.30	124
33	Broadcast	8 July	1.89	105
67	Broadcast	8 July	2.24	111
100	Broadcast	8 July	2.99	114
33	Deep placed	15 August	2.24	110
67	Deep placed	15 August	2.96	115
100	Deep placed	15 August	3.33	126
33	Broadcast	15 August	2.30	106
67	Broadcast	15 August	2.18	113
100	Broadcast	15 August	2.66	109

influence NH_3 volatilization. The differences between the performance of urea-containing fertilizers in the northern and southern Great Plains may be due to more humid night conditions in the north which contribute to heavier amounts of dew, possibly affecting NH_3 volatilization losses.

In the central Great Plains and Southwest, comparisons of N sources for wheat have occasionally indicated advantages to N applications which place the N below the surface residue layer and into moist soil. Usually those applications involve anhydrous NH_3. Better performance from anhydrous NH_3 placed at depths of 10 to 15 cm could be due both to lowered immobilization of N by decaying residues and to positional availability, and also to greater nutrient availability because of the presence of soil moisture in the fertilizer application zone. Data in Table 6D–9 indicate such a situation.

In summary, as long as reasonable precautions are followed, with special attention to local recommendations for time, source, and method of application, growers can expect efficient and comparable results from N fertilizers in areas of lower rainfall.

6D–1.1.5 Methods of Application

Broadcast applications of N for wheat (Fig. 6D–2) have been effectively utilized in low rainfall regions for both pre-plant and topdressed applications. Advantages include speed of operations and greater access to custom application services. However, broadcast applications are more subject to problems of NH_3 volatilization losses, positional unavailability due to poor incorporation and low rainfall and greater chances of organic matter immobilization.

Deep banding (>10 cm depth) of pre-plant fertilizer N below the seed zone has been shown to be more efficient than unincorporated broadcast applications (Campbell et al., 1984; Dahnke, 1983; Goos, 1983; Parsons and Koehler, 1984; Tomar and Soper, 1981) (Fig. 6D–3). Deep banding is particularly useful in reduced tillage systems where tillage for N fertilizer incorporation is difficult or not desirable and large concentrations of crop residues have accumulated on the soil surface (these may immobilize applied N during microbial decomposition of the residues) (Tomar and Soper, 1981).

The development of application equipment compatible with tillage operations has been a significant factor in the wide adoption of deep banding of N in the central Great Plains. The combined operations save fuel and labor plus providing the advantage of deeper placement in moist soil and penetration of the surface residues without immobilization (Tomar and Soper, 1981). Deep application of N, P, and other nutrients has proven to be feasible and agronomically advantageous. That procedure is discussed later.

Fig. 6D–2. Broadcast N applications for wheat have been attractive because of the availability of custom application services and the ability to cover large areas quickly. An additional advantage to broadcast N applications is the opportunity to combine application of herbicides and N solutions.

Fig. 6D–3. Application equipment for deep placement of nutrients. A wide range of tillage equipment has been adapted for simultaneous application of anhydrous NH_3 and liquid mixed fertilizer. This practice is common in the Great Plains area of the USA and Canada. Courtesy: TVA.

Fig. 6D–4. No-till drills have expanded the opportunities for combined seeding and fertilization operations. With specialized equipment, it is possible to apply the entire fertilizer program for wheat at the time of seeding, particularly in low rainfall areas of the western USA and Canada. Courtesy, Yielder Drill, Inc.

The problems associated with too large a concentration of N in direct seed contact were discussed above. Recent advances in design of reduced-tillage or no-till seeding equipment (Fig. 6D–4) gives the added option of applying large amounts of N in any form at time of seeding. Paired row placement of seed allows for combinations of starter placement with

or near the seed and deep placement of N and other nutrients between the drill rows (Fig. 6D–5). Quick early growth coupled with positional availability of N and other nutrients makes this concept attractive.

Another technique for improving wheat responses to surface N applications is to dribble the N in a narrow, concentrated band near the seed row at planting or as a topdressed application (Fig. 6D–1). The dribble application method reduces the contact of the fertilizer N with the residues, particularly in reduced-tillage and no-till systems, and minimizes the microbial tie-up of N.

6D–1.1.6 Effects of Application Timing on Fertilizer Response

Greater responses to N and P fertilization are expected from early planting, relative to late planting, of spring wheat (Alessi et al., 1979; Black and Siddoway, 1977a). If adequate N is not available at the time wheat is tillering and determining its yield potential, yield responses to N and P fertilization can be disappointing (Black and Siddoway, 1977b; Pumphrey and Rasmussen, 1982). A fall application of N is generally as effective as a spring application on heavy-textured soils in the drier climates of the northern Great Plains and Pacific Northwest. Spring applications of N are recommended in areas with high winter precipitation or on coarse-textured soils, to avoid leaching loss (Dahnke, 1983; Johnson et al., 1984; University of Saskatchewan, 1981).

For winter wheat in low rainfall areas and with relatively modest yield goals, pre-plant N applications have been feasible. Frequent use of anhydrous NH_3 as an N source sometimes favors pre-plant applications because of deeper placement into moist soil. On the other hand, pre-plant N applications have been viewed with some skepticism in some low rainfall areas because of a fear of excessive water use and because

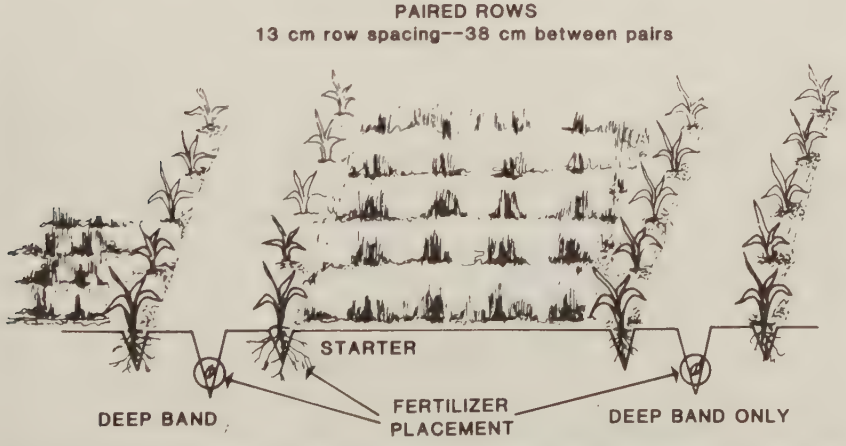

Fig. 6D–5. The use of paired rows with reduced or no-till drills combined with fertilizer application is compatible with deep placement and/or starter placement of nutrients. Deep placed nutrients are in close proximity to the plants. Courtesy, USDA-ARS.

of the uncertainty of the crop due to winter-kill and fall insect damage. The use of better moisture conservation practices and relatively low-cost N sources has made pre-plant applications much more acceptable and reduced the fear of early investment. Additional early N applications can benefit grazing of wheat by producing rapid, early season growth.

In higher rainfall areas and where wheat is grown on irrigated, sandy soils, concern over NO_3^--N leaching has prompted topdressed N applications in late winter or early spring. Excessive fall precipitation is rare in much of the semiarid region, but when it does occur, N losses can be significant and yields from pre-plant N applications will suffer (Table 6D–10). For the most part, however, fall and late winter (spring) N applications have been comparable. Delayed N applications tend to have a greater effect on grain protein and less on yield.

While late season N applications have been thought to affect mainly protein, some limited information does suggest that very late applications (growth stages 8 to 10 on the Feekes scale) may benefit grain yield as well as grain protein (Table 6D–11). Such late season applications are not routine in the region but are currently being researched in the context of seeking higher yields.

The strong relationship of grain protein to yield of hard red winter wheat was noted above (Goos et al., 1982). This particular relationship, which suggests that $<$ 12 g protein/kg of grain indicates a strong likelihood of yield loss (Fig. 6D–6), has been useful in convincing growers in areas where N use has been uncommon that supplemental N is needed.

6D–1.1.7 Grain Protein as Indicator of N Needs

Grain protein can be used as an indicator to evaluate a N fertilization program for hard red wheats (Goos et al., 1982; Goos, 1984; Massee and Painter, 1979). In North Dakota, Goos (1984) found that a spring wheat grain protein level below 140 g protein per kg grain indicates under fertilization with N. Goos et al. (1982) also found that a level of 120 g protein per kg grain indicated sufficient N for optimum yield of winter wheat.

Adding more N than needed for optimum yield will generally result in an increase in grain protein, as shown in Fig. 6D–7 (Christensen and Killorn, 1981; Fowler and de la Roche, 1984). Increased protein improves the milling and baking quality of hard red wheats used for bread (McGuire et al., 1974). Low grain protein in hard red winter wheat in the Pacific Northwest is common. Foliar applications of N have been shown to increase grain protein in this area (Altman et al., 1983).

6D–1.2 Phosphorus Mangement

6D–1.2.1 Phosphorus Soil Tests

A soil test is essential for establishing the need for P fertilization. Soil testing for P is the best way to monitor the residual effects of past

Table 6D–10. Topdressing N for winter wheat in late winter can improve N-use efficiency and yields when sandy soils are subjected to heavy fall precipitation in Kansas. Source: Gallagher et al., 1973b.

Nitrogen	Time N application	Sandy soil		Sandy soil		Silt loam soil	
		Yield	Grain protein	Yield	Grain protein	Yield	Grain protein
kg ha^{-1}		Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	g kg^{-1}
0	—	1.92	94	2.63	85	2.17	127
67†	Pre-plant	2.30	99	3.41	95	2.61	131
67	Late winter topdressed	3.18	120	3.62	98	2.64	134

†Means of 33, 67, and 101 kg N ha^{-1}, urea, sulfur-coated urea, and ammonium nitrate N sources.

Table 6D–11. Late season N applications (flowering) can increase both yield and grain protein content. Source: Gallagher, et al., 1977.

Pre-plant	Cultivar	Foliar N (Urea solution) kg ha $^{-1}$				Yield increase from foliar N	Percent increase from foliar N
		0		20			
N kg ha^{-1}		Yield Mg ha $^{-1}$	Protein g Kg $^{-1}$	Yield Mg ha^{-1}	Protein g Kg^{-1}	Mg ha^{-1}	
0	Lancota	2.03	120	2.61	126	0.58	28.6
0	Plainsman V	2.00	135	2.43	144	0.43	21.5
0	Centurk	1.83	122	2.46	126	0.63	34.4
0	Newton	1.68	127	2.15	130	0.47	30.0
33	Lancota	2.57	124	2.99	133	0.42	16.3
33	Plainsman V	2.55	137	3.00	138	0.45	17.6
33	Centurk	2.32	126	2.66	138	0.34	14.6
33	Newton	2.30	129	2.62	135	0.32	13.5
67	Lancota	2.74	130	2.92	136	0.18	6.2
67	Plainsman V	2.79	143	3.01	154	0.22	7.9
67	Centurk	2.47	143	2.80	140	0.33	13.3
67	Newton	2.61	135	2.95	136	0.34	13.0

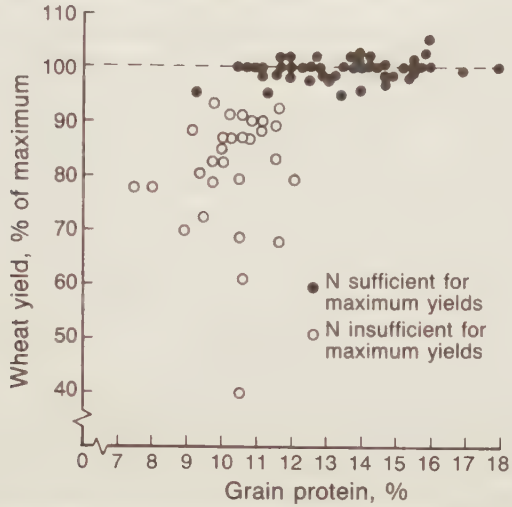

Fig. 6D–6. Grain protein has been found to be a good indicator of N nutrition adequacy for grain production in hard red winter wheat (Goos et al., 1982).

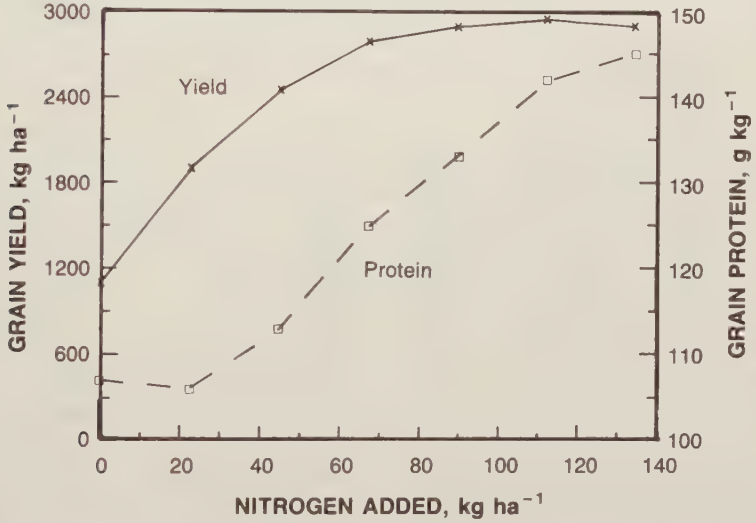

Fig. 6D–7. Average grain yield and protein content of three winter wheat cultivars (Winalta, Froid, and Centurk) grown in an annual cropping system (Halvorson et al., 1976).

P fertilization and future P needs of wheat. Soil samples for P analysis should be collected from the 0- to 15-cm soil depth. Sodium bicarbonate ($NaHCO_3$)-extractable P (Olsen et al., 1954) is the dominant soil test used on calcareous soils in the northern Great Plains of the USA and Canada. On moderately acid soils, the Bray-Kurtz weak acid extract is used to measure soil P availability. Soil test results for P may be erratic where fertilizer P has been previously banded in the soil, because the banded area may or may not be sampled when collecting soil samples. Collection of a larger number of soil samples per unit area may reduce the variability.

On calcareous soils, a sodium bicarbonate-extractable P level of more than 16 mg P per kg soil (high rating) is considered adequate for optimum wheat yields (Black, 1982; Dahnke, 1983). Wheat grown on soils with soil test P levels of < 10 mg P per kg soil, bicarbonate-extractable P (low rating) will generally respond to P fertilization. Approximately 5 kg P ha^{-1} is needed to increase the soil test level one unit on calcareous soils (Dahnke, 1983; Halvorson and Kresge, 1982). This may vary slightly, depending on soil texture and soil $CaCO_3$ content.

Bray-Kurtz soil test values on acid soils considered adequate for wheat range from about 25 mg kg^{-1} to as high as 50 mg kg^{-1}, depending on yield goal and location. Usually, higher soil test values are sought in the northern parts of the Midwest.

The use of yield goals for P recommendations varies more than for N recommendations. Phosphorus-use efficiency is relatively low, only about 15 to 20% of the applied P is used by the first crop. Placement can affect that percentage; it is discussed in more detail below. Phosphorus requirements are estimated for vegetative and grain portions of the wheat plant to be from 6 to 8 kg P Mg^{-1} grain. Phosphorus removed in the grain ranges from about 3 to 5 kg P Mg^{-1} of grain (F.E. Koehler, Department of Agronomy, Washington State University, 1986, personal communication; W.K. Griffith, Potash & Phosphate Institute, 1986, personal communication).

Taking into consideration the variations in classification of soils as very low, low, medium, and high, and considering the different methods of extraction and yields at which soil test correlation work was developed, the mean recommendations for P application per Mg of yield range from about 5 to just over 8 kg P ha^{-1} per Mg, assuming very low soil test P values, with a mean value about 6 kg P ha^{-1} Mg.

Soils of the semiarid regions are frequently low in P, which limits wheat yields substantially (Potash & Phosphate Institute, 1985). Responses to P are widespread and are well correlated to soil test P levels. For that reason, further consideration will be given to P management for wheat.

6D–1.2.2 Methods of P Application

In soils with low levels of available P, band applications of P either placed with the seed at planting or pre-plant are generally more efficient in the year of application than broadcast applications. On soils testing medium to high in available P, the difference in effectiveness between broadcast and band applications is minimal. At low soil test P levels (Fig. 6D–8), generally 1.5 to 3 times more fertilizer P is recommended for broadcast than band application to obtain the same yield goal (Alberta Agriculture, 1978; Dahnke, 1983; Peterson et al., 1981). Studies in Kansas (Fig. 6D–9), Colorado, and Oklahoma have provided similar evidence (Thompson, 1975; Kissel and Whitney, 1979).

Recent long-term P fertility studies have shown high rate (>90 kg P

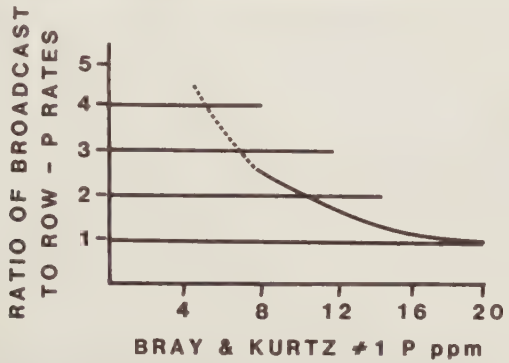

Fig. 6D–8. This figure shows a predictable and consistent relationship between efficiency of methods of P application for wheat and soil test levels for P. Row-applied P was about three times as effective as broadcast P at low P soil tests but the efficiency ratio was 1:1 when P tests were medium. This indicates that recommendations should change with soil test level (Peterson et al., 1982).

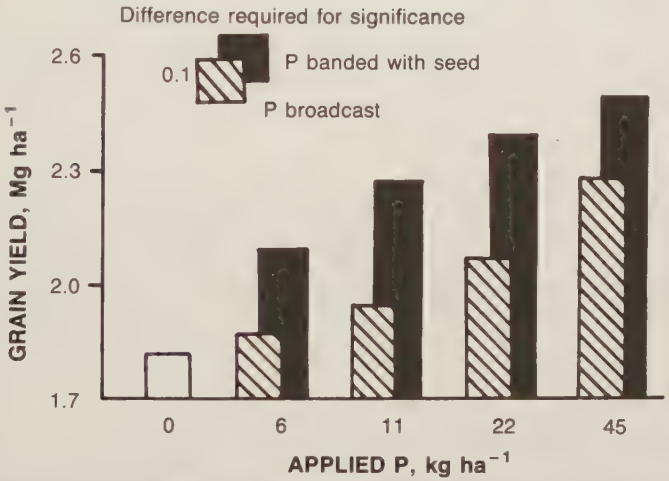

Fig. 6D–9. Kansas data indicate that band (seed) placement of P on low P-testing, neutral-to-alkaline soils improves P-use efficiency compared to broadcast applications (Thompson, 1975).

ha $^{-1}$), broadcast P fertilizer applications to be effective for more than 17 yrs (Halvorson and Black, 1985a, 1985b). Wagar and Stewart (1984) found that a single broadcast application of 80 kg P ha^{-1} resulted in a higher 5-yr yield average than 20 kg P ha^{-1} banded with the seed each crop year. Bailey et al. (1977) and Read et al. (1977) also demonstrated the long-term value of a single broadcast application of P fertilizer for wheat production. Jose and Nilsen (1982) concluded there was a long-term economic advantage of a single high rate broadcast P application over annual band P applications at several dryland sites in Canada. Adequate levels of available N are needed to get the full benefit from P fertilization, especially under annual cropping conditions (Halvorson and Black, 1985a).

A broadcast P application sufficient to bring the soil test level to 16 mg P kg^{-1} soil in the 0- to 15-cm depth on calcareous soils would be an effective way to assure optimum wheat yields under most environmental conditions. Smaller annual band applications with the seed would then be recommended to maintain the soil test level near 16 mg P kg^{-1} soil. This type of P fertilizer management program along with adequate N and water would probably result in optimum or near maximum wheat yields each crop year. Eroded areas with low P levels could initially be fertilized with large quantities of P and then treated like the remainder of the field with respect to annual P applications. All broadcast fertilizer P applications should be incorporated into the soil to obtain the most efficient use of the applied P.

Deep placement of N and P has received a significant amount of attention recently in the Plains states of the USA and the Canadian Prairie provinces. Deep placement, pre-plant banding, or dual application of N and P have been used synonymously to describe placement of N and P into the same soil zone, usually at depths of 10 to 15 cm. This type of placement produces high concentrations of both N and P in the soil retention zone. The technique has been adapted to tillage implements with savings in time and fuel by combination of tillage and fertilization operations. Anhydrous NH_3 and solid and liquid fertilizers have been used successfully for deep placement.

Deep placement of N and P under both conventional and reduced tillage systems has frequently been more effective for wheat (Fig. 6D–10) than more conventional methods of application that place most of the N and P at different positions in the soil (Leikam et al., 1983; Goos, 1983; Penas and Sander, 1982; Harapiak and Flore, 1984; Murphy, 1985). Greater effectiveness of the applied N and P resulted in higher nutrient-use efficiency but, more importantly, in higher yields for a given rate of application (Table 6D–12).

6D–1.2.3 Nitrogen Effects on P Availability

The importance of NH_4^+-N in P-use efficiency has been recognized for years (Grunes, 1959; Miller and Ohlrogge, 1958). However, the presence of even higher concentrations of NH_4^+-N in the soil P retention zones with deep placement or pre-plant band placement of P improves P-use efficiency beyond that provided by the inclusion of NH_4^+-H in conventional ammonium phosphate formulations. Wheat yield increases of 270 to 540 kg ha^{-1} were noted (Leikam et al., 1979) from application of 0.6 kg ha^{-1} active ingredient nitrapyrin[1], in anhydrous NH_3 or UAN, in deep placement with a fluid P fertilizer (Table 6D–13). Nitrapyrin slows the conversion of NH_4^+-N to NO_3^--N and maintains high concentrations of NH_4^+-N in the soil P retention zone for an extended period.

[1]Nitrapyrin, or *N-SERVE*, a product of Dow Chemical USA, 2-chloro-6-trichloromethyl pyridine. Use of a company or product name does not imply approval or recommendation of the product by the authors' agencies, or the exclusion of others which may also be suitable.

Fig. 6D–10. Deep placement of N, P, and other nutrients has proven to be an effective application method for wheat. This study demonstrates the improved efficiency of N and P deep placement for hard red winter wheat in Kansas compared to identical rates of nutrients broadcast. Nitrogen was supplied as UAN, P was supplied as liquid APP. All nutrients were applied pre-plant. The yield difference was 0.8 Mg ha $^{-1}$. Courtesy, D.F. Leikam, Farmland Industries, Inc.

The extended presence of NH_4^+-N could affect P absorption by plants by producing a lower pH in the soil solution at the root surface as the NH_4^+ ions are absorbed and H^+ ions are exuded by the roots to maintain electrical neutrality, or by slowing normal P fixation reactions with soil components (Hanson, 1984; Hanson and Westfall, 1983).

6D–1.2.4 Phosphorus Sources

Mono- and diammonium phosphates (MAP and DAP: $NH_4H_2PO_4$ and $(NH_4)_2HPO_4$), ammonium polyphosphate solutions (APP), concentrated (or triple) superphosphate (TSP), phosphoric acid (H_3PO_4), and urea phosphates (UAP) are the most prevalent fertilizer P sources used. Comparisons of P sources have not indicated consistent differences in performance for wheat (Olson et al., 1956; Baker et al., 1970; Kelley et al., 1977; Murphy, 1979). Except for germination and emergence effects on high pH soils, there is little agronomic difference among the various P sources. On calcareous soils and under low soil water conditions, the rate of DAP and UAP placed with the seed should not exceed 11 kg N ha $^{-1}$. With good soil water conditions in the seed zone, the rate of these fertilizers placed with the seed could possibly be increased. Recent research in North Dakota shows that higher rates of N placed with the seed (up to 40 kg N ha^{-1}) may be possible even when using UAP (Deibert et al., 1985).

Starter fertilizers for wheat should contain some N, suggesting a choice

Table 6D–12. Deep placement of N and P for wheat often has been more effective than applications which separate most of the applied N from the P. Source: Leikam et al., 1978.

Method of P application	Kg P ha^{-1}							
	10		15		19		24	
	Grain	Plant P	Grain	Plant P	Grain	Plant P	Grain	Plant P
	Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	
P knifed pre-plant	3.56	1.8	4.03	1.9	4.70	2.2	4.03	2.3
P broadcast pre-plant	2.96	1.7	3.29	1.6	3.83	1.7	3.83	1.8
P banded at seeding	3.02	1.6	4.10	1.7	3.83	1.9	4.57	2.0
			Control, N only	2.35 Mg ha^{-1}	1.6 g P kg^{-1}			
			$LSD_{0.05}$	0.60	0.3			

N rate: 87 kg N ha^{-1}.
Soil test P = 3.5 Mg kg^{-1}, very low.
P Source: APP liquid.

Table 6D–13. Nitrification inhibitor (*N-Serve*) and N-P placement effects on nonirrigated winter wheat. Source: Leikam et al., 1979.

Kg N ha^{-1}	Nitrogen source†	Method N-P application‡	Grain yield	
			O P	20 kg P ha^{-1}
			Mg ha^{-1}	
84	NH_3 + N-SERVE	Knifed	3.97	5.07
84	NH_3	Knifed	3.99	4.20
84	UAN + N-SERVE‡	Knifed	3.11	4.26
84	UAN	Knifed	2.96	3.32
84	UAN + N-SERVE	Surface strip§	2.50	3.23
84	UAN	Surface strip	2.96	2.00
84	UAN + N-SERVE	Surface broadcast	2.49	2.88
84	UAN	Surface broadcast	3.40	3.96
0	—	—	0.85	—

†All P supplied as APP liquid.
‡UAN = urea-ammonium nitrate solution.
§Strip application—coarse stream of liquid fertilizer on soil surface followed by disking.

of ammonium phosphates over triple superphosphate for that type of placement. Except for starters, choice of a P source has to be made on the basis of adaptability to the equipment to be used for application, price, availability in the area, and availability of dealer and custom application services.

6D–1.3 Potassium and Chloride

6D–1.3.1 Potassium

Soils in the northern Great Plains and the Pacific Northwest of the USA are usually high in available K (Potash and Phosphate Institute Staff, 1985). However, some moderately coarse- or sandy-textured soils and highly leached soils are low in available K. Fertilization of wheat with K on these soils will usually result in a yield response (Button, 1978; Dahnke, 1983; Skogley, 1976; University of Saskatchewan, 1981; Walker, 1978). Predicting yield responses to K fertilization, particularly on soils testing high in available K, has been a problem in some areas of the northern Great Plains (Schaff and Skogley, 1982; Skogley and Haby, 1981). Generally, K fertilization of soils testing < 75 mg K kg^{-1} soil (ammonium acetate extractable) in the 0 to 15 cm depth will result in a significant increase in wheat yields. As the soil test level increases to > 150 mg K kg^{-1} soil, wheat will probably not respond to K fertilization (Dahnke, 1983; Button, 1978; Walker, 1978). On higher pH soils, at low K soil test levels, 33 to 56 kg K ha^{-1} is generally recommended for wheat, depending on the yield potential (Dahnke, 1983; McDole et al., 1978; Skogley, 1976; Walker, 1978). Potassium recommendations for the low testing category of more acid soils (<50 mg kg^{-1} exchangeable K) range from a low of 30 kg ha^{-1} K to as high as 160 kg ha^{-1} for yields in the vicinity of 6 Mg ha^{-1}. Removal in grain is about 5 kg K Mg^{-1}.

Seed placement or side banding is the most efficient means of ap-

plying low rates of K. If K fertilizer is placed with the seed, N plus K should not exceed 45 kg ha $^{-1}$ (University of Saskatchewan, 1981). Potassium chloride (KCl), potassium sulfate (K_2SO_4), and potassium sulfate-magnesium sulfate are the dominant sources of K used.

6D–1.3.2 Chloride

Use of the KCl source of K fertilizer has been shown to have a dramatic effect on the suppression of take-all root rot (*Gaeumannomyces graminis*) disease of wheat in the Pacific Northwest (Beaton, 1984; Christensen et al., 1981, 1982; Jackson et al., 1983b; Petrie and Brown, 1983; Taylor et al., 1983) with positive yield effects (Fig. 6D–11). Beaton (1984) reported that Cl^- has been shown to be effective in Oregon, Idaho, Montana, South Dakota, North Dakota, and the Canadian Prairie provinces for controlling or reducing the severity of several plant diseases. The severity of stripe rust and *Septoria* were also reduced by the application of KCl (Beaton, 1984).

The chloride ion has been shown to be the factor reducing the incidence of several plant diseases. Thus, past yield responses to K fertilization may not have actually been a response to K specifically, but rather a response to the suppression of some plant disease by the chloride ion. The exact mechanism by which the chloride affects specific plant diseases is not fully understood at this time. A rate of 40 to 45 kg Cl ha $^{-1}$ is

Fig. 6D–11. Applications of chloride can have significant effects on wheat growth and yield. This Oregon study demonstrates the effects of applied Cl. Plants on the right received Cl. Note the more upright stature of the plants' leaves. Oregon data has shown that Cl has a suppressive effect on root rots in wheat. Courtesy, Tom Jackson, Oregon State University.

recommended for banding with the seed at planting, or 80 to 140 kg Cl ha $^{-1}$ broadcast in early spring for control of take-all root rot in winter wheat in Oregon (Jackson et al., 1983b). The presence of the NH_4^+-N ion also was effective in reducing take-all root rot in winter wheat. Therefore, use of an NH_4Cl fertilizer source should be effective in reducing the severity of this disease in wheat (Taylor et al., 1983).

6D–1.4 Sulfur

6D–1.4.1 Sulfur Deficiency

Sulfur is frequently adequate for wheat production in the northern Great Plains. However, some well-drained, coarse-textured, low organic matter soils may be S deficient (Alberta Agriculture, 1981; Beaton and Soper, 1986; Dahnke, 1983; University of Saskatchewan, 1981).

In the Pacific Northwest, S deficiency in wheat occurs frequently, but is hard to predict based on soil test (Gardner and Nibler, 1984; Rasmussen and Allmaras, 1986). Plant analyses for S can also aid in diagnosing the potential need for S fertilization (Jackson et al., 1983a). A response to S fertilization would be expected when the soil test level for SO_4^{2-}-S is $<$ 3 mg SO_4^{2-}-S per kg soil in the 0- to 60-cm soil depth or the N/S ratio in the plant is $>$ 16:1 (Gardner et al., 1983; Gardner and Nibler, 1984; Jackson et al., 1983a; Rasmussen and Kresge, 1985). Field studies have shown that 11 to 14 kg S ha $^{-1}$ is sufficient to maximize the yields of soft white winter wheat in the Pacific Northwest (Harder and Thiessen, 1971; Rasmussen and Allmaras, 1986; Rasmussen and Kresge, 1986).

Sulfur is often limiting in annual cropping and reduced tillage systems in the Pacific Northwest. In this area, application of S fertilizers will generally increase wheat yields with these management systems where high levels of N fertilizer have been applied and no S has been applied in recent years (Jackson et al., 1983a; Rasmussen and Allmaras, 1986; Rasmussen and Kresge, 1986).

6D–1.4.2 Soil Testing

Although some laboratories offer soil tests and recommendations for S for wheat and other crops, positive correlation information is not very strong. Some soils in the low rainfall areas are high in SO_4^{2-}-S, since gypsum and the presence of large amounts of SO_4^{2-}-S can rule out needs for supplemental S applications. Soils containing $<$ 6 to 7 mg kg^{-1} of SO_4^{2-}-S could possibly respond to added S.

Higher yields of wheat coupled with a low S content in most fertilizers point to a need for more emphasis on S research and S fertilization in the future. Wheat contains about 1 to 1.5 g S per kg of grain. Recommendations range from 10 to 30 kg S ha^{-1} which approximates a 5:1 N/S ratio in the fertilizer. This ratio is sometimes used as the basis for recommendations in areas suspected of being S deficient because the

applied N rate has some relationship to the yield goal. It is only an approximation, but one that is fairly workable.

Irrigation water frequently contains significant amounts of S, and this source can be calculated into the total amount of supplemental S needed. Since the S in the water is SO_4^{2-}-S and already in solution, it is as available as that applied as fertilizer. Knowing the amount of water that will be applied and the S concentration in the water, the amount to be applied can be calculated. However, if irrigation is delayed until well into the plants' development, supplemental S from fertilizer should be considered where deficiencies exist, even if water does contain S.

6D–1.4.3 Sulfur Sources

Sulfur is usually supplied as $(NH_4)_2SO_4$ (ammonium sulfate), $(NH_4)_2S_2O_3$ (ammonium thiosulfate, liquid), NH_4S_x (ammonium polysulfide, liquid), urea ammonium sulfate, elemental sulfur, ammonium phosphate-sulfate, potassium sulfate, potassium sulfate-magnesium sulfate, and calcium sulfate. All SO_4^{2-} sources are readily available for plant uptake and the SO_4^{2-} anion is mobile in the soil; thus, the method of application is not critical. Elemental S must be provided as very small particles so that oxidation will proceed at an adequate rate to satisfy plant needs for the SO_4^{2-} anion. Dispersible forms of elemental S are available.

Since SO_4^{2-} does not readily react with soil components in most soils of the region, broadcast, deep banded, or topdressed applications are all acceptable. Seed placement of ammonium thiosulfate (12-0-0-26S) is discouraged in order to avoid seedling damage from the generation of free NH_3. Recommended rates of 10 to 20 kg S ha^{-1} can cause severe germination damage when applied in direct seed contact as ammonium thiosulfate. This does not imply that this material is not a good S source; it merely represents the same type of precautions as outlined above for urea placement with the seed. (Ammonium sulfate does not exhibit this characteristic.)

Some recent Kansas data have indicated significant wheat responses to S on sandy, low organic matter soils (Table 6D–14). Interestingly, the Kansas data have not indicated significant increases in grain S contents from S fertilization although plant tissue S concentrations did increase.

Table 6D–14. Sulfur responses in wheat in the southern Great Plains and Southwest are usually associated with sandy soils, low in organic matter. Source: Lamond et al., 1984.

Main effects	Grain yield
	Mg ha^{-1}
Check	3.02
S rate, kg ha^{-1}	
17	3.50
34	3.53
S source	
Ammonium thiosulfate	3.41
Ammonium sulfate	3.60

The location received a total of 78 kg N ha^{-1}. Sandy soil, low in organic matter.

6D–1.5 Magnesium

6D–1.5.1 Wheat Tetany

Although some soils in the semiarid region are low in Mg, little information exists which relates wheat yield responses to applied Mg. More attention has been focused on the relationship of low plant Mg on wheat tetany in grazing animals. Harms (1976), Lamond (1978), and Karlen (1978) have extensively researched the relationships of N, K, and Mg fertilization to the composition of wheat forage, with the general conclusion that it is very difficult to modify the composition of the wheat plant to the point that it is less prone to causing tetany in grazing animals.

6D–1.5.2 Methods of Application and Sources

Harms (1976) reported that band applications of Mg wiith wheat seed at rates of 22, 45, and 67 kg Mg ha $^{-1}$ as $MgSO_4 \cdot 7H_2O$, $MgCl_2 \cdot 6H_2O$ and $MgNa_2EDTA$ were ineffective in terms of increasing Mg concentrations in wheat forage on three soil types. Foliar applications of 4.5 kg Mg ha $^{-1}$ as $MgSo_4 \cdot 7H_2O$ solution applied at seven-day intervals did maintain plant Mg levels above the critical 2 g Mg kg^{-1} level at one location. Adapted wheat cultivars differed significantly in Mg concentrations, but larger differences were noted in Ca and K concentrations and K/(Ca + Mg) ratios, which are directly tied to the tetany potential of forage.

Karlen (1978) studied the effects of applications of dolomitic limestone on dry matter production, nutrient composition, and grain yields of wheat in field experiments on two soil types. Dolomite ($CaCO_3 \cdot MgCO_3$) applied at a rate of 1140 kg ha $^{-1}$ containing 106 g Mg kg^{-1}, effectively increased the forage Mg concentration but increased the concentration only to 2 g Mg kg $^{-1}$ during the early growth stages. No significant reduction in the tetany potential of the wheat forage, as predicted by the equivalent ratio K/(Ca + Mg), was noted.

Lamond (1978) examined the effects of Mg applications, N form, N rate, and soil temperature on the tetany potential of winter wheat under both field and growth chamber conditions. Nitrogen form effects (NH_4^+ vs. NO_3^-) on plant Mg concentrations had been suggested by other authors (Ellis, 1979), but in field studies Lamond (1978) was unable to measure any consistent effects. Soil applications of Mg ranging up to 224 kg Mg ha $^{-1}$ had minimal effect on plant Mg contents, even though exchangeable Mg was as low as 60 mg Mg kg $^{-1}$. He concluded that Mg application to make wheat forage entirely safe from tetany problems in grazing animals was impractical.

6D–1.6 Micronutrients

6D–1.6.1 Zinc

Micronutrient problems in wheat in the western parts of the USA and Canada are relatively minor. Zinc deficiencies are possible on some

eroded or leveled soils where organic matter is low, but few research data show Zn responses in wheat. Soil deficiencies of Zn can be easily predicted by soil testing. Soils testing less than 0.3 mg kg $^{-1}$ of DTPA-extractable Zn would be considered to be possibly responsive to Zn, particularly under irrigated, high yield conditions. Zinc availability problems would be magnified by high soil tests for P. Sandy soils that are being intensively cropped (McKenzie, 1983; Moraghan, 1984; Dahnke, 1983; University of Saskatchewan, 1981) may be more subject to Zn deficiencies. Wagar and Stewart (1984) obtained a significant increase in wheat yield due to foliar application of Zn on a soil low in available Zn (0.5 mg per kg of DTPA-extractable Zn) that had been fertilized with more than 80 kg P ha^{-1}. However, at low P rates, Zn deficiency was not a problem.

Zinc sulfate and chelated forms of Zn would be the sources of Zn used to correct any Zn deficiencies in wheat. Soil and foliar applications of Zn would be effective.

6D-1.6.2 Iron

Some problems with Fe chlorosis in wheat have been reported from Oklahoma. Oklahoma recommendations indicate that when soil test values fall below 2 mg Fe kg $^{-1}$ (DTPA-extractable), chlorosis in wheat and other crops may occur. Crop sensitivity to Fe availability is increased when soil pH increases above 8.2 and soil test Mn levels are high (above 50 mg kg $^{-1}$ Mn). Foliar application of a 30 g kg $^{-1}$ $FeSO_4 \cdot 7H_2O$ (ferrous sulfate) (or ammonium ferrous sulfate) solution is effective for correction. Severe chlorosis may call for several applications. Effective control can be obtained from 2 kg Fe ha $^{-1}$ as a chelate or 9 kg ferrous sulfate per ha applied with ammonium polyphosphate solution banded near the seed. It is important to apply the polyphosphate and ferrous sulfate solutions in the same band (Johnson and Tucker, 1984).

6D-1.6.3 Copper

Copper is a problem for wheat grown on organic soils. Varvel and Grava (1983) point out that wheat often fails to reach maturity or does not yield satisfactorily on organic soils in Minnesota when supplemental Cu is not supplied. Copper deficiency symptoms in wheat are characterized by general yellowing of the plant, leaf tip dieback, and twisting of leaf tips. On severely Cu-deficient soils, growth ceases and the plant dies after reaching the tillering stage. Some severely deficient plants will produce a grainless head.

Using the DTPA extraction procedure, Minnesota scientists classify soils as low in Cu when soil test values are 0 to 2.5 mg kg $^{-1}$ Cu, marginal between 2.6 to 5.0 mg Cu kg^{-1} and adequate at Cu contents greater than 5 mg Cu kg $^{-1}$. Plant analysis can also be useful for determining deficiencies, but significant variation in concentrations can exist depending upon the stage of growth. When recently mature leaves contain < 4 to 6 mg Cu kg $^{-1}$ on a dry weight basis, the plant is likely to be suffering

from Cu deficiency. From 6 to 20 mg Cu kg^{-1} is considered to be sufficient. Greater than 20 mg kg^{-1} could indicate excessive or toxic accumulations. Wheat removes a very small amount of Cu from the soil, about 12 g Cu per Mg of grain.

Copper recommendations for organic soils are outlined in Table 6D–15. The most common Cu fertilizers available are $CuSO_4 \cdot 5H_2O$ (Cu sulfate), CuO (Cu oxide), and Cu chelates. Minnesota recommendations indicate equal effectiveness of these sources but point out that Cu chelates may be more effective (Varvel and Grava, 1983). Other sources (Follett et al., 1981) indicate about a 2:1 or 3:1 efficiency difference favoring chelates, compared to inorganic Cu sources. Copper chelates tend to be more compatible with liquid fertilizers.

6D–1.6.4 Manganese

Manganese, although deficient on some alkaline soils and on some poorly drained soils, is not recognized as a significant problem on wheat production in the semiarid regions of the USA and Canada.

6D–2 FERTILIZING WHEAT IN HUMID REGIONS

Wheat has long been an integral member of various crop rotations in the eastern USA. It has become increasingly significant in the southeastern USA in recent years due to adoption of rotations involving double-cropping of soybean or grain sorghum [*Sorghum bicolor* (L.) Moench] following wheat. Successful wheat production in the eastern USA involves careful cultivar selection, precision planting, weed control, insect control, disease control, possibly lodging control, timely harvest, and adequate fertilization. Fertilization in this humid region involves liming as well as the proper use of N, P, K, S, and micronutrients.

Soil testing provides the basis for predicting lime requirements and P and K needs in the humid areas of the eastern USA. Soil tests for N have been considered unreliable because of rainfall that moves NO_3^--N beyond the rooting zone in many sandy soils and causes denitrification in clay-textured soils. However, control of N application rates to avoid

Table 6D–15. Copper soil test interpretation and recommendations for organic soils in Minnesota. Source: Varvel and Grava, 1983.

Method of Cu application	Copper soil test (mg kg k^{-1})		
	0–2.5 low	2.6–5.0 marginal	> 5.0 adequate
Broadcast	7–13 kg ha^{-1}	7 kg ha^{-1}	None
Foliar	0.3 kg ha^{-1}	0.3 kg ha^{-1}	None

Broadcast applications are for copper sulfate, $CuSO_4 \cdot 5H_2O$. Copper chelates such as $CuNa_2EDTA$ may also be used. Chelates may be more effective, about 3:1 compared to copper sulfate. Higher Cu rates may be effective for 3 yr. Re-test after 3 yr. Foliar application: Copper sulfate solution at late tillering stage. It is effective only in the year applied.

groundwater contamination and provide an adequate inventory of N supplies for plants dictates further research in deep sampling for nitrates.

Soil tests are generally recommended every 2 to 4 yr, depending on soil textures, the more sandy soils being sampled every 2 yr and the silts and clays every 3 to 4 yr. However, many growers sample soils every year in order to closely monitor changes in soil pH, P, and K levels.

6D–2.1 Liming

Most soils in the eastern USA require the regular use of lime to neutralize soil acidity and to provide Ca and Mg for plant nutrition. Adams (1984) points out that liming is an essential component of a continuing and prosperous agriculture in the southern USA, while Lathwell and Reid (1984) indicate that the majority of soils in the northeastern USA require regular applications of lime for normal crop growth. In particular, the highly leached, weakly buffered soils of the coastal regions are especially subject to rapid pH changes resulting from natural processes and the use of ammoniacal-N fertilizers (Adams, 1984)

The detrimental effects of soil acidity have been adequately reviewed (Adams, 1984). These include Al toxicity, Mn toxicity, and Ca and Mg deficiency. Moreover, the detrimental effects on micronutrient availability from excessively high pH levels caused by over-liming have been well established for many years (Mortvedt, 1972).

The problems of soil acidity and liming and the effects on wheat are discussed in detail in section 5C, above.

6D–2.2 Nitrogen

6D–2.2.1 Soil Testing

Soil testing for residual NO_3^--N as practiced in the semiarid wheat producing regions has not been successfully utilized in the humid eastern and southern regions of the USA and Canada. Rainfall moves NO_3^--N below the crop rooting zone in many soils during most years. Stanford (1982) pointed out that basing N fertilizer recommendations on short-term N mineralization measurements has been relatively unreliable, because of the presence of varying amounts of residual mineral N from previous fertilization, even in humid regions. Moreover, the relatively low cost of fertilizer N has discouraged the development of N soil tests aimed at achieving more effective use of N fertilizers. Extensive recent research (60 field experiments) with N soil tests in Pennsylvania by Fox and Piekielek (1983) using maize as the test crop led to the conclusion that field-measured N-supplying capabilities of the soils were significantly correlated with several N-availability indexes, but the best correlation was so poor ($r \simeq 0.5$) that none of the tests would be useful in predicting N-availability in the field. Roth et al. (1984), working with wheat in Pennsylvania, concluded that N accumulated in soils from manure ap-

plications and previous fertilization makes efficient N management in this region virtually impossible.

The variable success of using soil N determinations to assist in making recommendations for N application require further study. Inclusion of several parameters such as depth of sampling for NO_3^--N, soil organic matter levels, and history of earlier fertilizer use, including manure applications, may be necessary to account for soil accumulations of N and to avoid excessive N applications when intensive wheat management is undertaken.

6D-2.2.2 Nitrogen Recommendations

The current situation in the humid eastern USA with regard to N fertilizer recommendations for wheat is that the results of field experiments on varying soil types and under local climatic conditions form the basis for N recommendations; soil tests for N are not currently utilized. Also, yearly weather patterns (e.g., excessive rainfall, producing either leaching or denitrification) are taken into account by farm advisors to modify local recommendations.

Recommended N fertilizer rates generally range between 80 and 112 kg N ha^{-1} throughout the region, although several individuals indicate that newly released cultivars have yield potentials that require increased N rates (personal communications from W. Sabbe, University of Arkansas, 1984; J.A. Herbek et al., University of Kentucky, 1984; M.A. Jackson, 1984, Rutgers University; C. Harms, Purdue University, 1984; D. Lee, University of Georgia, 1984).

6D-2.2.3 Time of Application

The influence of winter rainfall on N fertilization of winter wheat was recognized by Doll (1962), who reported that 20 to 23% of the deviation of winter wheat yields from the linear regression of yields on years in long-term Kentucky experiments could be attributed to winter rainfall. His research showed that under Kentucky climatic conditions the major portion of N fertilizer for winter wheat should be topdressed in the spring.

Welch et al. (1966) reported that during a three-yr study on a Cisne silt loam soil in Illinois, the relative efficiency of fall-applied N averaged 67% that of spring-applied N, but that the relative efficiency of fall-applied N increased with increasing N rates. Similar results were found in Arkansas by Sabbe (1978) who concluded that highest yields were obtained with topdressing wheat after it breaks dormancy in mid- to late winter.

More recent work by Hargrove et al. (1983) in Georgia showed that fall N applications up to 44 kg N ha^{-1} did not significantly affect yields, but that spring applications of 66 kg N ha^{-1} were needed to optimize yields on a Greenville sandy clay loam in the Coastal Plain and on a Cedarbluff silt loam in the Valley region. Spring N applications were also found to produce higher yields in Kentucky research with recently re-

leased cultivars (Herbek et al., 1984). Applications were most effective when made in March or April, since earlier treatments had a significant risk of N loss by leaching or denitrification but later treatments were ineffective.

Overall, most N recommendations specify applying 20 to 30% of the total N recommended at planting, with the remainder topdressed in late winter or early spring. Exceptions to this generalization occur when wheat is following well-fertilized crops such as tobacco and cotton or a legume. In these situations pre-plant N is not recommended (Miley et al., 1982; Anonymous, 1984; W.F. Faw, Louisiana State University, 1984, personal communication).

6D-2.2.4 Use of Nitrification Inhibitors

The development of effective nitrification inhibitors and the difficulty of making spring N applications because of wet soil conditions in many years has prompted experiments with fall application of the total wheat N requirement in combination with a nitrification inhibitor. Boswell et al. (1976), working with a Norfolk loamy sand and a Cecil sandy loam over a three-yr period found that an at-planting N application of 28 kg N ha^{-1}, plus 56 kg N ha^{-1} in the early spring, produced higher wheat yields than an 84 kg N ha^{-1} at-planting application, even with the nitrification inhibitor nitrapyrin. The inhibitor influenced the retention of NH_4^+-N in the surface soil for approximately 2 months, but N levels in spring tissue samples were not affected by inhibitor treatments. The addition of a nitrification inhibitor to fall-applied N produced 6.5% greater yields than fall-applied N without inhibitor, under Kentucky conditions (Murdock, 1984). However, wheat yields from spring-applied N fertilizer were 20% greater than similar fall-applied rates.

In contrast, Huber et al. (1980) found that differences in yields obtained with fall-applied N stabilized with nitrapyrin, as compared to a split application of N in the fall and spring without the use of a nitrification inhibitor, were generally not significant. These researchers were working with two Mollisols and two Alfisols in Indiana. Similar results have been obtained in seven more recent Indiana experiments conducted by Harms (1984, unpublished data) and in southern Illinois work by Liu et al. (1984). Also, a series of 10 experiments in Missouri between 1979 and 1983 indicated that pre-plant N applications with nitrapyrin were as effective as split fall and spring treatments (Hanson et al., 1984).

These somewhat contradictory results for fall applications of the total wheat N requirement with a nitrification inhibitor vs. a split fall plus spring application are reasonable when soil and climatic differences are taken into account. The Corn Belt soils generally have higher cation exchange capacities than the more highly weathered, lower organic matter content soils in the southern and eastern Piedmont and Coastal Plain regions. Soils with higher cation exchange capacity (CEC) have a greater capacity to retain NH_4^+, and thus nitrification inhibitors are more likely

to be effective. Also, soil temperatures remain higher throughout the winter in the southern and eastern coastal regions, favoring nitrification and negating benefits from the fall use of a nitrification inhibitor.

6D-2.2.5 Use of Plant Analysis

Difficulties of soil tests for N under humid region conditions have led to several projects evaluating plant tissue N content during spring growth as a means of assessing wheat N requirements. An extensive wheat tissue testing program is currently under way in Arkansas (865 fields in 1984), with growers making sequential spring N applications based on tissue N contents at various growth stages (D. Adams, University of Arkansas, 1984, personal communication). This program is being refined and details are expected to be published in the near future.

In Virginia, analysis of whole wheat plants collected at Feekes growth stage 5, and flag leaf samples taken at Feekes growth stage 10 indicated an N sufficiency range of 40 to 50 g N kg^{-1} for obtaining maximum yields of recently released wheat varieties (Donohue and Brann, 1984). Hargrove et al. (1983) suggested a 35 g N kg^{-1} sufficiency level for flag leaf samples collected at flowering, Feekes growth stage 10.5. More recent Virginia experiments have confirmed that a 40 g kg^{-1} N concentration in the aboveground whole plant samples at Feekes growth stage 5 is associated with 90% maximum yields (Gravelle, 1983; M.M. Alley, unpublished data).

6D-2.2.6 Nitrogen Sources

The most widely used N fertilizer sources in the region for wheat are urea [$(NH_2)_2CO$] anhydrous NH_3, urea-ammonium nitrate (UAN) solutions, and ammonium sulfate [$(NH_4)_2SO_4$]. These sources are generally rated as being equal for providing N for wheat growth (Miley et al., 1982; Segars, 1982; Basking and Anderson, 1983; Thom et al., 1981; J.R. Jared, University of Tennessee, 1984, personal communication). The UAN solutions have the potential for burning foliage during spring applications and thus are not recommended for use if air temperatures are greater than 21° C and rates are $>$ 50 kg N ha^{-1} per application of 320 g kg^{-1} (32%) N solution (Baskin and Anderson, 1983). Rates of 90 kg N ha^{-1} supplied as 30% N UAN solution produced no foliar burning of wheat tissue in a 1984 Virginia experiment (Alley et al., 1984) but resulted in significant tissue dessication in 1985 (M.M. Alley, unpublished data). Weather and fertilizer solution characteristics associated with foliar burning from UAN applications are not well defined at this time.

Current N fertilization information has been developed almost solely with management systems producing yields ranging from 1.5 to 4.0 Mg ha^{-1}. Average yields in the region range from 2.5 to 3.0 Mg ha^{-1}. However, research with management systems utilizing new varieties, narrow row spacings, and disease, insect, weed, and lodging control have produced yields ranging from 7.0 to 9.0 Mg ha^{-1} in several areas. These high

yields have generally been obtained with pre-plant N applications in conjunction with at least two spring N applications. Rates and timings of N fertilization have yet to be refined for the most efficient and economical program. However, it is most likely that N fertilization recommendations will be significantly different for more intensive management production systems, compared to lower yielding programs.

6D–2.3 Phosphorus

6D–2.3.1 Soil Testing

Phosphorus fertilizer requirements for wheat production are evaluated by soil testing in all areas. The two most commonly used soil test procedures for plant-available P are the Mehlich-1 (0.05 *M* HCl + 0.0125 *M* H_2SO_4) and the Bray-1 (0.03 *M* NH_4F + 0.025 *M* HCl) methods. Kamprath and Watson (1980) summarized numerous experiments dealing with these soil test procedures and reported that the critical level for plant response to applied P is between 25 and 30 mg kg^{-1} for the Bray-1 procedure but that the critical level for the Mehlich-1 test varies with soil texture. Plant growth increases to applied P are generally not observed when Mehlich-1-extractable P levels are greater than 10 mg kg^{-1} on clayey soils, while on sandy soils the critical extractable P level ranges between 20 and 25 mg kg^{-1}.

The amounts of fertilizer P needed to increase soil test levels have been published by Peck et al. (1971), Griffin and Hanna (1967), and Cope (1981). However, due to the long history of P fertilization of most crops in the eastern USA, most agricultural soils test in the medium to high level of plant-available P. For example, 64% of soil samples tested in Virginia prior to planting wheat in 1983 tested high in Mehlich-1-extractable P (Donohue, 1984). Thirty-one percent tested in the medium range, and only 4% were low in plant-available P. All states recommend build-up P applications for those soils testing low in available P, but most P fertilization is now made for beneficial starter effects or maintenance of residual P levels.

6D–2.3.2 Methods of P Application

The beneficial effect of P placed with wheat seed at planting has been reported by Knapp and Knapp (1978). The silt loam soil in their central New York experiment had an initial Bray-1-extractable P level of 20 mg kg^{-1}. A 20 kg P ha^{-1} application banded with the seed increased winter survival and grain yields, especially when planting dates were delayed beyond the optimum for the location. Research with placement of preplant P on sandy loam soils in Virginia showed a yield increase from a 90 kg P ha^{-1} application when Mehlich-1-extractable P levels varied between 20 and 25 mg P per kg of soil (Alley and Brann, 1985). The 90 kg P ha^{-1} rate was the total P requirement for the wheat and the following double-crop soybean. However, all placement methods (including surface

band (strip), subsurface band, in-row, and broadcast) were equally effective for increasing wheat yields in their studies.

Sharpe et al. (1984), working with pre-plant broadcast P rates ranging from 0 to 384 kg P ha^{-1} found that a 64 kg P ha^{-1} treatment produced the highest wheat yields on a Cecil sandy loam soil testing low in plant-available P. Highest yields in the experiments were 3.1 Mg ha^{-1} and P rates greater than 64 kg P ha^{-1} were associated with increased disease (*Septoria nodorum*) and lodging.

6D–2.3.3 Phosphorus Sources

Diammonium phosphate (DAP), monoammonium phosphate (MAP), ammonium polyphosphate solutions (APP), and concentrated superphosphate (TSP) are the most widely used P fertilizers in the humid region of the USA and Canada. These materials have equal P-supplying abilities and the particular source utilized depends on cost and local availability. Also, P fertilizer applications prior to wheat planting usually include the P requirements for both the wheat and the following soybean or grain sorghum crop in those areas that practice double-cropping.

6D–2.4 Potassium

6D–2.4.1 Soil Testing

Many if not most soils in the eastern USA require supplemental K to produce optimum wheat yields. Soils in the region vary widely in K retention capacity and fertilization history. Soil testing is essential for evaluating the K-supplying status of individual fields.

The most widely used index of K availability is the neutral 1 *M* NH_4OAc-extractable K procedure (Knudsen et al., 1982), although several mid-Atlantic and Southeastern states use the Mehlich-1 method (Isaac, 1983). According to Knudsen et al. (1982) and Doll and Lucas (1973), these procedures recover about the same amount of K from most soils.

Crop yield responses from applied K are minimal when exchangeable K levels are greater than 85 mg K kg^{-1} soil for sands and loamy sands, 100 mg K kg^{-1} soil for sandy loams and loams, and 125 mg K kg^{-1} soil for silt loams and clays (Doll and Lucas, 1973). Most wheat fertilization recommendations call for building exchangeable soil K levels to the high soil test range, with recommended additions for low testing soils varying from 35 to 90 kg K ha^{-1} (Anonymous, 1984; Hoeft, 1984; Miley et al., 1982).

6D–2.4.2 Potassium Sources, Time of Application

Potassium chloride is the major source of K fertilizer in this region, although potassium-magnesium-sulfate is utilized if Mg and/or S are required. The total K fertilizer requirement is usually broadcast prior to planting wheat, but for deep, sandy soils with low cation exchange ca-

pacities the K requirement should be split equally between pre-plant and early spring applications (Segars, 1982). Also, all K fertilizer is normally applied prior to wheat planting in wheat double-crop soybean or grain sorghum cropping systems.

6D–2.5 Sulfur and Micronutrients

6D–2.5.1 Sulfur

Sulfur is recommended at the rate of 11 kg S ha^{-1} for wheat in Georgia (Segars, 1982), while North Carolina growers are advised to apply 25 kg S ha^{-1} to wheat grown on soils with sandy surface horizons greater than 40 cm in depth (R.E. Jarret, North Carolina State University, 1984, personal communication). Published data showing wheat yield response to S fertilization under field conditions are not available. Greenhouse research by Hue et al. (1984) indicated a critical total S concentration in wheat plants of 1.6 ± 0.1 g S $kg.^{-1}$. The critical value for Ca $(H_2PO_4)_2$-extractable SO_4^{2-}-S was estimated to be 6.0 ± 1.3 mg SO_4^{2-}-S kg^{-1} soil in the experiment.

6D–2.5.2 Micronutrients

Adequate supplies of micronutrients are available for wheat growth in most soils in the eastern USA. However, wheat is classified as being highly sensitive to Cu deficiency with yields possibly being reduced up to 20% without the appearance of obvious deficiency symptoms (Alloway and Tills, 1984). Younts (1964) determined that 2.8 kg Cu ha^{-1} were required for maximum wheat yields on two soils with widely differing organic matter contents. Comparable yields were obtained with copper sulfate and copper chelate (EDTA), with applications at planting or during late winter being effective in correcting Cu deficiencies. April applications were ineffective. Barnes and Cox (1973) confirmed these results with four field experiments on shallow Histosols.

More recently, Makarim and Cox (1983) obtained wheat yield responses to Cu fertilization in three of seven field experiments, and established a critical level of 4.0 mg Cu kg^{-1} for wheat flag leaves at early heading. Tissue analysis research by Martens (1976) indicated that 2.2 mg Cu kg^{-1} in 20-cm tall whole wheat plant samples collected in March was inadequate for maximum growth, but that a concentration of 2.9 mg Cu kg^{-1} was sufficient. Tissue Cu concentrations have also been shown to decrease linearly with increasing P rates up to 304 kg P ha^{-1} applied to a Cecil sandy loam soil (Touchton et al., 1980). Copper fertilization is not needed for most wheat, but high-yielding management programs and wheat grown on organic soils require careful attention to possible Cu needs.

The potential for both Mn toxicities and deficiencies in many areas of the southeastern USA prompted nutrient solution studies (Fales and Ohki, 1982) on the effects of low and high available Mn levels on wheat.

A critical tissue deficiency level of 35 mg Mn kg^{-1} was established, while concentrations of 475 mg Mn kg^{-1} in tissue were found to be toxic to wheat. These critical concentrations were associated with 10% reductions in dry matter yields. Field data on crop response are unavailable, but manganese sulfate is the fertilizer material most widely used for correction of deficiencies attributed to low Mn availability.

6E Wheat Stand Establishment

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Establishment of adequate wheat, *Triticum aestivum (L.),* stands is prerequisite for high grain yields. Adequate stands contain ample plants for potential yield levels, allow maximum returns from other production inputs, buffer against stand losses, and may decrease the need for practices such as chemical pest control. Deficient stands, on the other hand, limit grain yields and may increase the need for other production inputs. High-quality seed and suitable seedbeds usually assure good seed germination. The proper date and rate of seeding, seed placement, and row spacing are necessary, however, for a high percentage of seedling emergence and good stand establishment.

6E–1 DATE OF SEEDING

Optimum seeding dates for wheat have long been set by research and by growers' experience. Local recommendations are available from most experiment stations, and usual seeding dates have been compiled (Burkhead et al., 1965). Optimum dates for seeding winter wheat range from late August in the northern Great Plains (Fowler, 1982) to early November in the South (Reitz, 1976). Spring wheat is seeded from late autumn in the western USA (Reitz, 1976) to mid-May in Canada (Briggs and Aytenfisu, 1979).

Grain yield is usually the major criterion for designating optimum seeding dates for wheat (e.g., Alessi et al., 1979; Ciha, 1983; Knapp and Knapp, 1978). When forage for pasture is important, seeding dates for winter wheat may be advanced several weeks to promote vegetative growth. In arid regions, wheat is often seeded early according to moisture availability, not calendar date (Kolp et al., 1973). Winter survival is a paramount consideration in regions where cold causes high mortality of poorly hardened plants (Fowler, 1982). The seeding date for spring wheat

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is also governed by the need to avoid cold temperatures during critical early developmental stages and high temperatures during grain filling. In practice, however, actual seeding dates range widely because of the need for favorable weather conditions during planting (Bond and Umberger, 1979).

Temperature and moisture are major determinants of the response of wheat to seeding dates. Optimum temperatures are about 25 °C for germination (Lindstrom et al., 1976) and 16 °C for coleoptile elongation (Burleigh et al., 1965); nearly 100 degree-days after planting are needed for emergence (Rickman et al., 1983). Additional degree-days, 150 to 200, must accumulate before the three- to five-leaf stage that favors overwintering is reached. Exposure to low temperatures is nevertheless required for hardening and vernalization of winter wheat. Late-seeded wheat may not harden adequately and, in extreme cases, may not be vernalized.

Soil water potential near field capacity favors both germination and emergence of wheat (Lindstrom et al., 1976). The lower threshold of soil water potential for good emergence, approximately -1.5 MPa, increases with increasing temperature (Lindstrom et al., 1976). Soil temperatures between planting and emergence and soil water conditions between emergence and heading account for much of the yield difference between early and late-seeded spring wheat (Deschenes and Dubuc, 1981). Extremely early seeding of winter wheat is especially detrimental in arid regions because of depletion of soil water needed for later development (Kolp et al., 1973). Late seeding of winter or spring wheat increases the probability of blowing of dry soil and stress from high temperatures and moisture deficiency during grain development.

Improper seeding dates, either early or late, have many adverse consequences. Optimum seeding dates, on the other hand, encourage high seed germination, strong plants, and a vigorous root system in all wheats and prostrate growth and high winter survival in winter wheat (Reitz, 1976). Timely seeding also favors tillering and well-timed phenological development (Musick and Dusek, 1980), reduces lodging, and increases most grain yield components and test weight (Alessi et al., 1979; Briggs and Aytenfisu, 1980; Ciha, 1983; Knapp and Knapp, 1978). Water-use efficiency and fertilizer recovery are also highest with optimum seeding dates (Alessi et al., 1979; Black and Siddoway, 1977a; Kolp et al., 1973; Musick and Dusek, 1980). Grain protein and moisture contents may be increased by late seeding, but flour yield and baking absorption are decreased (Alessi et al., 1979).

Many disease and pest hazards compound adverse effects of untimely seeding. Hessian fly (*Mayetiola destructor* Say), aphids (*Schizaphis graminum* Rond.), take-all (*Ophiobolus graminis* Sacc.), *Septoria* leaf spot, powdery mildew (*Erysiphe graminis* DC.), leaf rust (*Puccinia recondita* Rob. ex Desm.), *Fusarium* snowmold, *Fusarium* scab, *Fusarium* root rot, *Cercosporella* foot rot, spindle streak mosaic virus, wheat streak mosaic virus, and yellow dwarf virus, for instance, may be more prevalent with

early than late seeding (Gates, 1975; Huber, 1979; Reitz, 1976). Some diseases, however (e.g., *Rhizoctonia* snowmold, *Typhula* snowmold, bunt [*Tilletia* spp.], leaf rust, and mildew), may be more severe after late seeding (Huber, 1979; Smid and Jenkinson, 1979). Early seeding fosters weeds such as *Bromus* spp. in winter wheat and wild oats (*Avena fatua* L.) in spring wheat, whereas sparse crop canopies from late seeding favor many other weed species (Bond and Umberger, 1979; Reitz, 1976).

Selection of optimum seeding dates is a compromise among adversities, but is nonetheless an effective component of a pest management program (Huber, 1979). Adjusting seeding dates to control specific pests without regard to other factors may not be feasible, however, since combatting pests by altering the seeding date may lead to greater reductions in grain yield from untimely seeding than from pests (Gates,1975).

6E–2 RATES OF SEEDING

Environmental effects, numerous interactions with other factors, and compensatory mechanisms in wheat cause wide ranges of optimum seeding rates for wheat. Expression of seeding rates as mass or volume per area, however, is also partly responsible for imprecise recommended seeding rates. Seeding by mass or volume can affect plant densities 50% or more (Puri and Qualset, 1978) because of differences in seed size. Considering the variation in seed size of many new cultivars and the precision required in production practices for high yields, we hope that seeding rates will be expressed in seed numbers per area in the future.

Recommended seeding rates in Canada and the USA, using seed weighing 34 g 1000^{-1}, range from 67 seeds m^{-2} in the dryland plains to 400 seeds m^{-2} in eastern regions of North America (Reitz, 1976). The most widely recommended rate, 200 seeds m^{-2} (67 kg ha^{-1}, or one bushel per acre), is used for northern Great Plains spring wheat, central Great Plains winter wheat, Pacific Northwest spring and winter wheats, and southwestern USA spring wheat. This basic rate is increased for local conditions by about 50% for irrigation, 25% for pasture, and 10% per week of delay in seeding after the optimum date.

Grain yields respond parabolically, rising rapidly, plateauing over a wide range, and declining slowly as plant density increases (Willey and Heath, 1969). Different wheat yield components are affected as interplant competition increases. Plants per area limit yields at low seeding rates, although most other yield components are at their highest level. Tillers per plant and yield per tiller interact to cause a broad plateau in grain yield as seeding rate increases (Briggs and Aytenfisu, 1980; Smid and Jenkinson, 1979). Spike density, kernels per spike, or kernel weight determines maximum yield in different cultivars (Faris and DePauw, 1981). Interplant competition reduced yields at excessive seeding rates, mainly by depleting soil moisture under low-yield environments and by inducing

lodging under high-yield environments (Ciha, 1983; Kolp et al., 1973; Roth et al., 1984).

Cultivar responses to seeding rates reflect intraplant competition in the extensive environment at low densities and interplant competition at high densities (Faris and DePauw, 1981). The plant structure approaches the monoculm ideotype as density increases (Roth et al., 1984), but lodging may nevertheless increase and limit grain yields (Ciha, 1983). Lodging resistance clearly is crucial for wheat cultivars planted at high seeding rates in favorable environments. Because modern wheat cultivars may express a yield advantage only at high seeding rates (Faris and DePauw, 1981), improvements in yield potential must be accompanied by greater lodging resistance.

Environmental resources and cultivar characteristics influence the optimum seeding rate for wheat. Low seeding rates give maximum yields when environmental conditions are limiting (Read and Warder, 1982). Favorable environments, particularly for moisture, temperature, and nutrients, support high plant densities for high grain yields (Roth et al., 1984).

Most present seeding rate recommendations for low-yield environments appear satisfactory (Baker, 1982; Kolp et al., 1973). Seeding rates might even be reduced substantially in certain cases (e.g., when high rates are used to control weeds, a task better accomplished by herbicides) (Read and Warder, 1982). Inadequate seeding rates, however, can cause buildup of weed populations even in crops that follow wheat (Vander Vorst et al., 1983).

Under high-yield environments, current seeding rates frequently fail to produce maximum grain yields. Higher seeding rates might be necessitated by high-yield management practices (Roth et al., 1984), late seeding after double-cropping (Smid and Jenkinson, 1979), specific requirements of certain cultivars (Baker, 1982), and the need for high rates for maximum yields of modern cultivars (Faris and DePauw, 1981). Extensive testing to determine optimum seeding rates is mandated by cultivar $\times$ seeding rate interactions (Faris and DePauw, 1981) and location-to-location and year-to-year inconsistencies (Baker, 1982).

6E–3 SEED PLACEMENT

A seeding depth of 2 to 4 cm is nearly universally optimum for wheat when soil moisture is adequate for stand establishment. Deep seeding (8 to 12 cm) is usually practiced only when soil moisture is deficient at shallower depths. Beyond 10 to 12 cm, seedling emergence is poor (Torres and Paulsen, 1982). If moisture is inadequate at that depth, seed should be "dusted in" at least 5 cm to prevent germination from light rains that cannot sustain growth. Deep furrow drills or mulch hoe drills can be used to place seed where moisture is available without excessive coverage by soil (Fenster et al., 1977).

Extremely shallow or deep seeding hinders establishment of adequate wheat stands. Shallow seeding results in poor seed coverage by soil, inadequate moisture for germination, and development of plant crowns near the soil surface where they are susceptible to heaving and lodging (Roth et al., 1984). Deep seeding causes low seedling emergence, weak plants, and uneven stands (Rickman et al., 1983).

Soil moisture is the single most important factor in wheat seeding depth, but soil temperature, texture, and surface conditions also must be considered (Burleigh et al., 1965; Fenster et al., 1977; Lindstrom et al., 1976; Reitz, 1976). Plant factors that influence the desirable seeding depth include coleoptile length, emergence rate, and seed size and protein content (Allan, 1980; Fick and Qualset, 1976; Puri and Qualset, 1978; Torres and Paulsen, 1982).

Seeding depth is more critical for dwarf and semidwarf than for tall cultivars because of differences in coleoptile length. All *Gai* (*Rht*) genes tested reduce coleoptile length of wheat seedlings, directly or pleiotropically (Fick and Qualset, 1976). Short coleoptiles also slow seedling emergence rate and decrease total seedling emergence, particularly with deep seeding (Allan, 1980). Seeding depths that give satisfactory stands of tall cultivars may give sparse stands of dwarf or semidwarf cultivars.

Coleoptile length of wheat can be increased genetically within the same general height class. It is unlikely, however, that semidwarf genotypes with the long coleoptiles of tall genotypes can be developed. Semidwarf genes have unfavorable effects, even when incorporated into genetic backgrounds with favorable properties (Allan, 1980), and coleoptile lengths of progeny of crosses between different height genotypes segregate transgressively toward the shorter parent (Fick and Qualset, 1976). Most success might come from accumulating modifier genes that favor stand establishment (Allan, 1980).

Wheat seed size and protein content might also be increased to enhance stand establishment. Large seeds produce better stands than small seeds, at least in part because seedling coleoptiles are longer, and favor high grain yields (Puri and Qualset, 1978). Increasing seed protein content has the same effect, especially in semidwarf genotypes, because it increases the rate and percentage of seedling emergence at most seeding depths (Torres and Paulsen, 1982). Both seed size and protein content correlate highly with seedling vigor, which is related to grain yield because plant density is a major yield component (Evans and Bhatt, 1977).

6E–4 ROW SPACING AND DIRECTION

Row spacing for wheat is determined largely by the environmental resources that influence seeding rates. Optimum row spacings range from 10 to 15 cm in regions where seeding rates are high to 35 cm where deep furrow drills are used with low seeding rates. Two opposite trends in row spacings are evident: narrow rows for intensive management (Oplinger

and Wiersma, 1984) and wide rows for conservation tillage and intercropping systems (Chan et al., 1980; Fenster et al., 1977).

The ideal equidistant spacing for low interplant competition is approached in narrow rows at a given seeding rate. Increasing the seeding rate increases both interplant competition and the advantages of narrow rows. Broadcasting, largely discarded because of its many disadvantages, theoretically distributes seed more favorably than drilling. In practice, however, compensation among yield components usually causes negligible grain yield differences among a wide range of row spacings.

The greatest benefit from narrow rows occurs when soil moisture is high (Chan et al., 1980; Roth et al., 1984). Under low soil moisture, substantial differences in row spacing may not affect grain yield (Ketata et al., 1976; Vander Vorst et al., 1983). Even then, narrow rows can increase tiller density (Ketata et al., 1976) and improve weed control in crops that follow wheat (Vander Vorst et al., 1983).

Plant characters, particularly stature and leaf angle, also influence wheat response to row width (Stoskopf, 1967). Narrow rows may be required for wheat to benefit from these features, which may be disadvantageous in wide rows.

Wheat grain yields are typically higher in east-west rows than in north-south rows (Day et al., 1976; Erickson et al., 1979; Kirkham, 1982). Reasons for this difference are not well understood. Row orientation perpendicular to prevailing winds might increase stress and harvest index of wheat and decrease wind erosion (Erickson et al., 1979). Spike density and kernels per spike are also higher in east-west rows (Day et al., 1976). Plants in north-south rows, on the other hand, intercept more light and produce more vegetative growth (Erickson et al., 1979; Kirkham, 1982). Cross-drilling, however, gives the same grain yields as unidirectional drilling (Ketata et al., 1976).

6E–5 STAND ESTABLISHMENT FOR INTENSIVE MANAGEMENT

Intensive management for high yields, as practiced in other wheat-producing regions of the world, is being adopted in North America (Oplinger and Wiersma, 1984; Roth et al., 1984). Departures from recommended practices for stand establishment are few, however. The most prominent are elevated seeding rates, narrow rows, and tramlines for equipment travel for applying fertilizers, pesticides, and growth regulators.

Seeding rates of about 550 kernels m^{-2} and row spacings of 8 to 10 cm to ensure ample plants are advocated for winter wheat in the Great Lakes region (Oplinger and Wiersma, 1984). Tramlines are formed by closing one or two drill openings at intervals determined by the width of equipment used for subsequent operations. Their effect on grain yield is usually negligible, because compensation by plants in rows adjacent to tramlines offsets their loss.

6F Water Relations and Irrigation

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6F–1 IRRIGATED WHEAT ACREAGE

Wheat, *Triticum aestivum (L),* is adapted to a wide range of climatic conditions, evidenced by its wide distribution in the USA and the world. It is grown extensively in arid regions, where water is often the primary yield limiting factor. In these areas wheat yields can be sharply increased by irrigation. Irrigating wheat is a science, as is the management of soil profile water for wheat production where irrigation water is not available. The timing of irrigations and the application of the lowest amount of water for optimum yields are of primary importance for both wheat production and water conservation where the competition between agriculture and other uses of limited water supplies continues to grow.

The irrigated wheat area in the 17 Western states more than doubled from 790 000 ha in 1964 to 1 823 000 ha in 1982. This represents 5.2 and 8.3% of the total area seeded to wheat in those states, respectively, for those years. The total area seeded to wheat was approximatley 35 Mha in the USA, of which 22 Mha were in the 17 Western states, including essentially all of the irrigated area (U.S. Census of Agriculture, 1964, 1982) (Table 6F–1). The portion of the wheat area irrigated, although increasing, is small but important, because of the high wheat yields that can be produced under irrigation.

6F–2 WATER RELATIONS AND IRRIGATION SCHEDULING

Extensive research has been conducted to determine the optimum time or growth stage to irrigate to obtain maximum yields of high quality wheat. Two basic approaches have been investigated. One approach is

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Table 6F–1. Total and irrigated wheat area in the 17 Western states. Source: 1964, 1974, and 1982 U.S. Census of Agriculture.

State	Total area (1000 ha)			Irrigated area (1000 ha)			Percent irrigated		
	1964	1974	1982	1964	1974	1982	1964	1974	1982
Arizona	11	71	54	11	69	54	100	97	100
California	108	285	375	33	152	290	30	53	77
Colorado	615	1 149	1 156	34	51	82	6	4	7
Idaho	422	572	610	120	177	266	28	31	44
Kansas	3 659	4 471	4 720	95	154	290	2	3	6
Montana	1 516	1 915	2 111	36	27	67	2	1	3
Nebraska	1 105	1 144	1 046	8	15	48	1	1	5
Nevada	8	11	8	8	11	8	100	100	100
New Mexico	57	83	194	22	37	41	38	44	21
North Dakota	2 538	4 127	3 974	3	5	9	0.1	0.1	0.2
Oklahoma	1 660	2 404	2 417	24	48	65	1	2	3
Oregon	312	506	478	22	50	66	7	10	14
South Dakota	841	1 222	1 349	1	3	6	0.1	0.2	0.4
Texas	1 266	1 413	2 059	303	357	363	24	25	18
Utah	82	107	96	18	22	16	22	20	17
Washington	847	1 224	1 099	49	121	145	6	10	13
Wyoming	86	123	144	3	4	7	3	3	5
Total	15 133	20 827	21 890	790	1 303	1 823	5	6	8

to irrigate at definite crop growth stages, and the other is to irrigate when the moisture available to the crop has been depleted to some precalculated value, irrespective of growth stage, until maturity.

Several researchers have suggested that wheat has stages in its development that are not equally sensitive to moisture stress. An extensive review by Salter and Goode (1967) concluded that the internode elongation (or shooting) and heading stages of wheat growth are particularly sensitive to moisture stress and that irrigations after the soft dough stage do not increase yields. Robins and Domingo (1962) found that moisture deficits during or after heading of spring wheat resulted in appreciable grain yield reductions because fewer heads, fewer spikelets, and fewer kernels per spikelet were formed. Day and Intalap (1970) reported that yield losses were greatest when spring wheat was water stressed at the jointing growth stage. Water stress at this stage also resulted in fewer heads and fewer kernels per head.

In studies on winter wheat, Schneider et al. (1969) and Hooker et al. (1983) determined that adequate soil moisture is necessary from the jointing/booting stage through heading. Water stressing winter wheat during vegetative growth limits leaf and tiller development, while stress during the jointing stage accelerates stem senescence and reduces the number of spikelets per head (Musick and Dusek 1980). Singh (1981) ranked the winter wheat growth stages in decreasing sensitivity to moisture stress as: (i) booting/heading, (ii) flowering to grain development, and (iii) vegetative. He concluded that where the irrigation water supply is limited, irrigation should be timed so that water deficits are distributed evenly over the growth stages before the most critical booting/heading stage. This water deficit distribution produces a wheat crop better suited to future water stress and minimizes yield loss.

The second major irrigation scheduling method is based on evapotranspiration (ET), or the water loss to the atmosphere through evaporation from the soil and transpiration from the crop. Evapotranspiration and related soil moisture measurements can be determined using large weighing lysimeters, pan evaporation, soil moisture blocks, tensiometers, and neutron probes.

A weighing lysimeter consists of a soil tank supported on a sensitive mechanical platform scale. A reference crop is grown on the area surrounding the lysimeter, and in the lysimeter tank. Weight changes resulting from ET, precipitation, and irrigation are recorded throughout the growing season, along with other meteorological measurements. Crop coefficients, such as those developed by Wright (1982) from this method, can then be used to estimate actual water use at progressive growth stages for a particular crop from measurements of the reference crop ET. Crop coefficients are used in computerized irrigation scheduling programs such as the USDA-ARS Irrigation Scheduling Program described by Jensen et al. (1971). This program provides estimates of when to irrigate and how much water to apply, using climate, crop and soil data.

Pan evaporation (PAN-E) is calculated as the cumulative evaporation from a U.S. Weather Service Class A open-pan less rain since the previous irrigation. Prihar et al. (1976) have suggested using the ratio between irrigation water (IW) and PAN-E as a practical guide for scheduling wheat irrigation. For optimum yields, an IW/PAN-E ratio of 0.75 to 1.00 is recommended when two preconditions are met: (i) wheat is planted after a presowing irrigation, and (ii) the first irrigation is applied 25 to 30 days after sowing. In comparing the IW/PAN-E approach to the common practice of irrigating at five growth stages (crown rooting, tillering, jointing, booting, and grain filling), Prihar determined that an IW/PAN-E ratio of 0.75, irrespective of growth stage, resulted in grain yields as high as those based on irrigating at five growth stages. Irrigation at an IW/PAN-E ratio of 0.75 also resulted in the highest water expense efficiency (kg of grain per ha cm water), thus conserving irrigation water.

Stored soil water at planting time determined with soil moisture blocks, tensiometers, or neutron probes is an important parameter in the water relations of both irrigated and dryland wheat production. Brown et al. (1981) developed relationships of wheat yields to stored soil moisture plus growing season rainfall for the northern Great Plains. Their results provide guidelines for assessing the probabilities of a successful crop based upon the amount of stored water in the soil. Wheat usually will not produce grain in that region with stored water of < 10 cm. Each unit of stored soil water above 13 cm will produce an incremental wheat yield increase. The quantity of stored soil water is also important in irrigated areas with insufficient water supplies. The greater the amount of stored water, the lower will be the irrigation requirements for a successful crop.

Scheduling irrigations based on climate and crop and soil data provides many potential benefits to the farmer. Foremost is increased net return through increased yields and lower production costs. Secondary benefits include increased water-use efficiency, reduced irrigating labor costs, and elimination of detrimental effects associated with poor irrigation practices such as over- or underirrigation (Jensen 1970). Overirrigation may result in reduced yields caused by diseases, lodging, and nutrient leaching. Conversely, continual application of irrigation water less than the crop ET can result in deleterious accumulations of soluble salts in the crop root zone.

6F–3 IRRIGATION METHODS

The method or system used to supply irrigation water to restore depleted soil water is important to irrigated wheat production. The method must provide for water application according to the schedule that will avoid soil water depletion to the point of crop water stress. If the application method does not meet this requirement, efforts should be made to improve it, since otherwise scheduling procedures have little value towards producing optimum yields.

Four irrigation methods are typically used to irrigate wheat: border-strips, basins, furrows, and sprinklers. The first three are gravity systems and require no energy except when pumping may be required to lift water from wells, rivers, or lakes into a canal system.

Border-strip irrigation is accomplished by dividing a field into a number of strips separated by low levees or borders. Water enters the upper ends of these strips from a supply ditch or other source and flows freely as a sheet toward the lower ends. The land betwen the levees, perpendicular to the direction of water flow, must be level for the water to cover the entire width of the strip. The slope in the direction of water flow from the upper to lower end can be up to 3% for wheat, but this method works best when the slope is 0.2 to 0.4% (Hansen et al., 1979). Advantages of the border-strip method include high water application efficiencies, low labor requirements, low maintenance costs, and a wide adaptability to soil types. Limitations may include extensive initial land grading, a need for engineering design for high efficiences, availability of required large water flows, and hindrance of cultivation and harvesting by levees (Bishop et al., 1967).

The basin irrigation system requires a field to be divided into level areas bordered by levees or dikes. Water is turned in at one or more points until the desired volume is applied. Advantages of basin irrigation include high application efficiences, uniform application and leaching, erosion control, and low maintenance costs. Limitations include high initial costs of extensive land grading and dike construction, and reduced cultivation and harvesting efficiences because of the dikes or levees.

Wheat may also be irrigated by parallel furrows down slope. In some areas, small furrows are called *corrugates*. Furrow depth and spacing can vary. Typically, wheat is drilled with row spacing ranging from 15 to 35 cm. It may be drilled with rows in the same direction as the irrigation furrows or at any angle to the furrow direction. Water is supplied to each furrow through small openings in a supply ditch, siphon tube, gated pipe, or (in the recently developed cablegation systems) small controlled opening in a pipe (Kemper et al. 1981; Goel et al. 1982). Furrows are spaced 76- to 102-cm apart, and as a result, only about one-fourth or less of the surface is utilized for water infiltration. Water generally must flow in furrows for several hours after the stream reaches the lower end to allow sufficient infiltration time to replenish depleted water over the entire run length. Water sets of 12 and 24 h are common in many areas. Water infiltration is often greater than needed to meet ET demands near the upper ends of fields because water is present for infiltration longer there than at lower ends. As a result, uneven water distribution and extensive nutrient leaching may occur. Furrow irrigation is also rather labor intensive except where automated systems have been installed. Soil erosion can be severe with furrow irrigation where slopes exceed about 1% (Berg and Carter 1980). Also, with the furrows, the field surface is rough and causes more wear and breakage to cultivating and harvesting equipment.

However, irrigation is adaptable to small water supplies as well as larger ones, because the set, or number of furrows simultaneously irrigated, can be adjusted, and furrow irrigation can be used on lands that are too uneven to irrigate by border or basin methods.

Sprinkler irrigation has gained popularity since 1975. This method has increased 69% from 1973 to 1983 in the 17 Western states (Goldstein, 1984). Currently, the most widely used system is the center pivot, followed by towline/sideroll systems. Hand move systems are declining in popularity, because they are labor-intensive. Solid set or permanent systems are still less widely used. Guns, booms, and linear move systems represent a small portion of the systems in use today. Linear move systems have good potential. Sprinkler systems have many advantages over gravity systems. Water can be applied to the entire land surface at a rate lower than the infiltration rate so that no erosion occurs. Application efficiencies can be high. Implements have been developed to make thousands of small basins per hectare on steeply sloping land to trap water applied by center pivot sprinklers and markedly increase wheat production (Longley, 1984). Automated sprinkler systems require little labor. The most serious drawback to sprinkler irrigation is the escalating power costs, and these costs are projected to continue to rise.

Current research is underway to reduce energy requirements for sprinkler irrigation by increasing pumping plant efficiencies and reducing water losses from leaks, worn nozzles, etc. Low pressure systems have been developed and are in production. These systems use low pressure heads, and larger pipes than conventional systems to reduce friction losses. Even with these systems, energy costs for sprinkler irrigation continue to rise.

6G Weed Control in Wheat

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Weeds have been a major factor in the management of wheat, *Triticum aestivum (L),* since commercial production began. With the trend toward shorter cultivars and the use of higher rates of N fertilizers, weeds may be even more competitive than in years past.

Yield losses caused by weeds may be due to competition or allelopathy. *Competition* occurs when some necessary factor — primarily water, light, or nutrients — becomes limiting. Agronomists often inaccurately generalize that the most severe competition occurs early and therefore early weed control is required (Zimdahl, 1980). This statement may be true with spring wheat under dry soil conditions, but studies on winter wheat often show that wheat and weeds can co-exist for several weeks or months without significant wheat yield loss as long as no factor necessary for growth becomes limiting and none of the weeds are allelopathic. For example, Rydrych (1974) showed that uncontrolled downy brome (*Bromus tectorum* L.) reduced winter wheat yield by 40% (wheat seeded in October), but if the downy brome was removed by February, no significant yield loss occurred. In a study in western Oregon (Brewster et al., 1977), a dense stand of Italian ryegrass (*Lolium multiflorum* Lam, 3200 plants m^{-2}) reduced yields from 6500 kg ha^{-1} in weed-free plots, compared to 800 kg ha^{-1} in the untreated control; yet when weeds were removed in early December, yields were not significantly higher than when the weeds were not removed until in late January. Clearly, the period of the wheat growth cycle at which weeds reduce yields depends on which factor is limiting and thus must be analyzed for each situation.

Allelopathy is the inhibition of one plant by another through the release of chemicals. Although not extensively studied in wheat, allelopathic effects from a wide variety of plants have been noted (Rice, 1974; Putnam and Duke, 1978) and probably account for some of the wheat yield loss when weeds are present.

Weeds can be detrimental in several ways besides reducing yields. Grain contaminated with weeds or weed seeds brings a lower price when sold. Off-flavor weeds, such as wild garlic (*Allium vineale* L.), may reduce

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flour quality. Weeds may interfere with the harvest operation or may raise the moisture content of the harvested grain, leading to heating and pest incidence in storage.

6G–1 CONTROL METHODS

6G–1.1 Manual Control

In some countries where labor is plentiful and the weeds are used for food or livestock feed, hand weeding is a common method of weed control in wheat. This method is seldom used in the USA and Canada because of high labor costs and extensive acreages; however, hand weeding still may be the most practical approach when weed densities are low and scattered, or when the wheat is being grown for seed and other methods are inadequate.

6G–1.2 Cultural Control

A great deal of weed control can be accomplished through the use of common-sense farming practices. Indeed, before the 1940s, when 2,4-D and MCPA were introduced (Table 6G–1), growers depended almost entirely on intelligent cultural practices to keep weeds to a minimum.

A cheap and easy way to reduce weed problems is to use weed-free seed. Buying weed-infected seed at a reduced price can prove to be poor economics in the long run, especially if new weed species are introduced into the farmer's fields.

A reduction in weed density may be accomplished by manipulating

Table 6G–1. Chemical names of herbicides.

Common name	Chemical name
Barban	4-chloro-2-butynyl-*m*-chlorocarbanilate
Bromoxynil	3,5-dibromo-4-hydroxybenzonitrile
Chlorsulfuron	2-chloro-*N*-[(4-methoxy-6-methyl-1,3,5-triazin-2-yl) aminocarbonyl] benzenesulfonamide
Dicamba	3,6-dichloro-*o*-anisic acid
Diclofop-methyl	2[4-(2,4-dichlorophenoxy)phenoxy]-methylpropanoate
Difenzoquat	1,2-dimethyl-3,5-diphenyl-1*H*-pyrazolium
Dinoseb	2-(*sec*-butyl)-4,6-dinitrophenol
Diuron	3(3,4-dichlorophenyl)-1,1-dimethylurea
Glyphosate	*N*-(phosphonomethyl)glycine
Linuron	3(3,4-dichlorophenyl)-1-methoxy-1-methylurea
MCPA	4-chloro-2-methylphenoxy acetic acid
Metribuzin	4-amino-6-(1,1-dimethylethyl)-3-(methylthio)-1,2,4-triazin-5(4*H*)-one.
Paraquat	1,1′-dimethyl-4,4′-bipyridinium ion
Picloram	4-amino-3,5,6-trichloropicolinic acid
Terbutryn	2 *tert*-butylamino-4-ethylamino-6-methylthio-*s*-triazine
Triallate	*S*-(2,3,3-trichloroally)diisopropyl-thiocarbamate
2,4-D	(2,4-dichlorophenoxy)acetic acid

time of seeding. The success of this approach is unpredictable, because it requires the proper weather conditions. In areas in which wheat is seeded with a deep-furrow or shovel-type drill, the wheat may be planted to moisture, leaving the surface layer too dry for weeds to germinate. If subsurface moisture is adequate and the surface remains dry, the wheat may gain a strong competitive advantage over the weeds by early seeding. However, in some areas, early seeding may aggravate insect and disease infestations.

Conversely, seeding may be delayed to allow as many weeds as possible to germinate. These then can be destroyed by tillage or herbicides before seeding the crop. This method is effective when (i) the weather cooperates by providing good germination conditions for the weeds, and (ii) a high percentage of the weed seeds are nondormant and germinate quickly. Unfortunately, delaying seeding beyond the optimum planting time sometimes reduces wheat yield potential.

The density of some weeds in wheat may be reduced or the buildup of weeds avoided by crop rotation. Weeds which have a life cycle similar to wheat tend to represent the most severe problems. For example, hardy winter annuals such as cheat (*B. secalinus* L.), downy brome, jointed goatgrass (*Triticum cylindricum* (Host) Ces.), and Italian ryegrass can be serious problems in winter wheat because they can germinate and grow at the same time as the wheat. Summer annuals such as pigweeds (*Amaranthus* spp.), lambsquarters (*Chenopodium album* L.), foxtails (*Setaria* spp.), wild buckwheat (*Polygonum convolvulus* L.), and many others are common weeds in spring wheat. Wild oats (*Avena* spp., primarily *A. fatua* L.) are among the world's worst weeds in cereals and can infest both winter and spring wheat.

A weed infestation can be reduced by rotating to crops with a different life cycle or ones in which different cultural and chemical practices are used. For example, in the Great Plains, rotation from winter wheat to grain sorghum can be effective in reducing an infestation of annual brome species. Seeds of the annual bromes are relatively short-lived (Chepil, 1946); only a few survive beyond 2 yrs, so preventing seed formation for two consecutive seasons is usually sufficient (Finnerty and Klingman, 1962). Crop rotation is, of course, less effective against weeds in fields infested with large numbers of long-lived seeds.

Management practices which encourage a healthy and vigorous wheat crop will tend to reduce losses from weeds. Some of the practices may include proper seeding depth; seeding at the appropriate time; correct amount, timing, and placement of fertilizers; using adapted cultivars; controlling insects and diseases; and skillful management of soil moisture, perhaps by fallowing or drainage. Unfortunately, not all good management practices are conducive to maximum weed control. Many excellent cultivars are semidwarfs, but these shorter cultivars usually are more adversely affected by weeds than are tall cultivars (Appleby et al., 1976). In some cases, weeds may respond to fertilizer at least as much as wheat

does, leading to actual wheat yield losses from fertilizing unless weeds are controlled in some other way (Appleby et al., 1976). Wide row spaces are recommended in some areas for moisture management, but leaving more open space between rows can reduce competition against the weeds. Clearly, controlling weeds by cultural practices alone is not simple and requires not only astute management by the grower, but often favorable weather conditions as well.

6G–1.3 Chemical Control

Selective chemical control of weeds in wheat with H_2SO_4 and several inorganic salts was used as early as the late 1800s. These materials were contact-type herbicides which often were corrosive, limited in selectivity, and strongly influenced by environmental conditions. The first organic selective herbicides for wheat were the dinitrophenol compounds, introduced in the 1930s. The discovery of the phenoxy herbicides, primarily 2,4-D and MCPA, in the early 1940s opened up a whole new concept in selective weed control. These compounds are translocated within the plant and therefore have the ability to kill larger annual weeds and many perennial weeds. They are less sensitive to weather conditions than previous herbicides. These traits led to immediate widespread use of these herbicides. Increasingly favorable prospects for herbicide markets for the phenoxy herbicides sparked a search for new selective herbicides which remains unchecked to this day. Appleby (1980) reported that approximately 48 herbicides were being marketed somewhere in the world for use on wheat, although many of these were not registered for use in the USA. With the trend toward minimum tillage and no-till systems, herbicide use will become even more widespread in the future.

The availability of herbicides has proven to be a tremendous boon to wheat growers. Control programs can be carried out much more quickly using herbicides than by mechanical means, thus improving timeliness of the application and flexibility in management. Control of deep-rooted perennial weeds, such as field bindweed (*Convolvulus arvensis* L.), although still imperfect, has improved greatly. However, chemical control should be viewed as an additional tool, not as a panacea. The very efficiency of the herbicides has led to heavy dependence on chemicals alone, often to the exclusion of mechanical and cultural control methods. When one control method is used continuously, whether it is mechanical or chemical, a more resistant weed population can build up. In some cases, resistant *biotypes* within a species can be selected for, and can increase in numbers. More commonly, resistant *species* can replace sensitive ones which have been eliminated by the herbicide. This can be avoided by integrating as many control measures, such as crop rotation, as possible; by using mixtures of herbicides with different mechanisms of action; and by rotating herbicides from one season to the next.

Some of the principal herbicides used in U.S. wheat (Table 6G–1)

are briefly discussed below. Several others are used primarily for local problems.

6G–1.3.1 Broadleaf Control

Dicamba, picloram, 2,4-D, and MCPA are growth-regulator type chemicals used for control of annual or perennial broadleaf weeds. They are applied to the foliage and can be translocated to the roots. The least injury to the wheat is obtained by applying after the wheat is well-tillered but before the stem begins to elongate (jointing stage).

Bromoxynil is effective against many small annual broadleaves. It is primarily a contact herbicide and, therefore, is ineffective against large weeds or perennials. It can be used safely on seedling wheat, when growth-regulator herbicides should not be used.

Chlorsulfuron is highly active on a wide range of broadleaf weeds and a few grasses at rates of 8 g ha^{-1} or even lower. Although it degrades in the soil, both by microbial and nonbiological means, minute amounts of residues in the soil can injure sensitive crops so it must be used with care in fields that will be rotated to non-cereal crops. Chlorsulfuron is less persistent in acid soils than in neutral or basic soils.

6G–1.3.2 Grass Control

Several herbicides have been developed primarily for the control of wild oats in wheat. These include triallate, barban, difenzoquat, and diclofop-methyl. Some of these herbicides also are effective against other grass weeds as well. For example, diclofop-methyl is highly active against Italian ryegrass and also controls foxtails and barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.]. Under optimum conditions it also can control blackgrass (*Alopecurus myosuroides* Huds.) and littleseed canarygrass (*Phalaris minor* Retz.).

This group of herbicides illustrates the variety of application methods and timings used for wheat herbicides. Triallate is usually applied before or after planting and mechanically incorporated into the soil before wheat emergence. Some success has been achieved by applying it postemergence in granular form. Barban must be applied when most of the wild oats are in the two- or three-leaf stage. Difenzoquat may be applied up to the five-leaf stage. Diclofop-methyl controls wild oats more effectively when applied post emergence, but it is more effective on downy brome and blackgrass when applied pre-emergence or to very small weeds.

6G–1.4 General Weed Control

A few herbicides are effective against both broadleaf and grass weeds. These include metribuzin, diuron, linuron, and terbutryn. These are all active through root uptake, as well as some foliar uptake, and often are strongly influenced by soil characteristics. All of these herbicides are more

phytotoxic to both weeds and wheat on sandy soils or soils with less than 1% organic matter.

Glyphosate and paraquat are non-selective herbicides which may be used to destroy emerged weeds anytime before the wheat emerges.

In addition to the above herbicides, more than 30 other herbicides are used in wheat elsewhere in the world. Several experimental herbicides for wheat are under study at any given time, and the number of herbicides available is expected to grow. In all cases, the label for each specific product should be closely followed.

REFERENCES

Adams, F. 1984. Crop response to lime in the southern United States. *In* F. Adams (ed.) Soil acidity and liming. 2nd ed. Agronomy 12:211–265.

Adams, E.P., E.J. Williamson, P. Carson and R. Gelderman. 1978. Fertilizing wheat. Coop. Ext. Serv., South Dakota State Univ. FS 677.

Alberta Agriculture. 1978. Phosphorus fertilizer application in crop production. Publications Office, Alberta Agriculture, Edmonton. Agdex 542–3.

----1981. Alberta fertilizer guide. Publications Office, Alberta Agriculture, Edmonton.

Alessi, J., J.F. Power, and L.D. Sibbitt. 1979. Yield, quality and nitrogen fertilizer recovery of standard and semidwarf spring wheat as affected by sowing date and fertilizer rate. J. Agric. Sci. 93:87–93.

Allan, R.E. 1980. Influence of semidwarfism and genetic background on stand estaablishment of wheat. Crop Sci. 20:634–638.

Alley, M.M., and D.E. Brann. 1986. Ammonium polyphosphate placement for soft red winter wheat. 1985 Fluid Fertilizer Found. Symp. Proc., Fluid Fertilizer Foundation, Peoria, IL.

----, ----, and J.L. Hammons. 1984. Maximum yield wheat research, *In* D.E. Brann and M.M. Alley (ed.). Results from small grain intensive management studies in 1984. Virginia Polytechnic Institute and State Univ. Pub. 424–020.

Allmaras, R.R., A.L. Black, and R.W. Rickman. 1973. Tillage soil environment and root growth. p. 62–86. *In* Conservation tillage. Soil Conservation Society of America, Ankeny, IA.

----, E.A. Hallauer, W.W. Nelson, and C.D. Evans. 1977. Surface energy balance and soil thermal property modifications by tillage-induced soil structure. Minn. Agric. Exp. Stn. Tech. Bull. 306.

Alloway, B.J., and A.R. Tills. 1984. Copper deficiency in world crops. Outlook on agriculture. 13:32–42. Pergamon Press, London.

Altman, D.W., W.L. McCuistion, and W.E. Kronstad. 1983. Grain protein percentage, kernel hardness, and grain yield of winter wheat with foliar applied urea. Agron. J. 75:87–91.

Anderson, D.T. 1961. Surface trash conservation with tillage machines. Can. J. Soil Sci. 41:91–114.

----. 1964. Some factors affecting trash conservation with disk-type implements. Can. Agric. Eng. 6:1–13, 19.

----. 1965. Some factors affecting trash conservation with heavy-duty cultivator. Can. Agric. Eng. 7:45–46, 49, 56.

----. 1967. Factors affecting trash conservation with a wide-blade cultivator. Can. Agric. Eng. 9:98–100, 127.

----. 1968. Some qualitative effects of tilling machines on plant residues used for erosion control. Can. Agric. Eng. 10:53–56.

Anonymous. 1984. 1984–1985 lime and fertilizer recommendations. Univ. of Kentucky, Ext. Publication AGR-1, Lexington.

Andrews, W.B. 1954. The response of crops and soils to fertilizers and manures. 2nd ed. Mississippi State University, State College, MS.

Appleby, A.P. 1980. Weed control in rain-fed wheat. p. 324–327. *In* Proc 3rd Int. Wheat Conf., Madrid, Spain. 22 June–3 May 1980. USAID/USDA/Univ. Nebraska, Lincoln.

----, P.D. Olson, and D.R. Colbert. 1976. Winter wheat yield reduction from interference by Italian ryegrass. Agron. J. 68:463–466.

Army, T.J., A.F. Wiese, and R.J. Hanks, 1961. Effect of tillage and chemical weed control practices on soil moisture losses during the fallow period. Soil Sci. Soc. Am. Proc. 25:410–413.

Bailey, L.D., E.D. Spratt, D.W.L. Read, F.G. Warder, and W.S. Ferguson, 1977. Residual effects of phosphorus fertilizer. II. For wheat and flax grown on chernozemic soils in Manitoba. Can. J. Soil Sci. 57:263–270.

Baker, J.M., B.B. Tucker, and L.G. Morrill. 1970. Effects of sources of phosphorus under varying soil temperature and moisture regimes on the emergence of winter wheat. Soil Sci. Soc. Am. Proc. 34:694–697.

Baker, R.J. 1982. Effect of seeding rate on grain yield, straw yield and harvest index of eight spring wheat cultivars. Can. J. Plant Sci. 62:285–291.

Ball, W.S., and J.K. Larsen. 1985. Winter wheat survival — No-till planting gives the needed edge. Crops Soils 37(8):21–23.

Barnes, J.S., and F.R. Cox. 1973. Effects of copper sources on wheat and soybeans grown on organic soils. Agron. J. 65:705–708.

Barnes, O.K., and D.W. Bohmont. 1958. Effect of cropping practices on water intake rates in northern Great Plans. Wyo. Agric. Exp. Stn. Bull. 358.

Baskin, C.C., and K.L. Anderson. 1983. Wheat fertilization. Mississippi State Univ. Agron. Dept. Inf. sheet 1217.

Bauer, A., and A.L. Black. 1981. Soil carbon, nitrogen, and bulk density comparisons in the two cropland tillage systems after 25 years and in virgin grassland. Soil Sci. Soc. Am. J. 45:1166–1170.

----, and T.J. Conlon. 1974. Effect of tillage interval of fallow on available soil nitrogen, some physical soil properties and wheat yields. N.D. Agric. Exp. Stn. Res. Rep. 51.

----, and H.L. Kucera. 1978. Effect of tillage on some soil physiochemical properties and on annually cropped spring wheat yields. N.D. Agric. Exp. Stn. Bull. 506.

----, E.H. Vasey, R.A. Young, and J.L. Oxbun. 1967. On non-fallowed soil — Stored soil moisture best guide to nitrogen needed. N. D. Farm Res. 24(11):15–24.

Beaton, J.D. 1984. Crop responses to potassium chloride: Due in part to chloride? Proc. 6th Annual Manitoba-North Dakota Zero Tillage Workshop, Bismarck, ND. 26–27 Jan. 1984. North Dakota State University, Department of Soil Science, Fargo.

----, and R.J. Soper. 1986. Plant response to sulfur in western Canada. *In* Sulfur in agriculture. Agronomy: 27:375–399.

Berg, R.D., and D.L. Carter. 1980. Furrow erosion and sediment losses on irrigated cropland. J. Soil Water Conserv. 35:267–270.

Bishop, A.A., M.E. Jensen, and W.A. Hall. 1967. Surface irrigation systems. *In* R.M. Hagen et al. (ed.) Irrigation of agricultural lands. Agronomy 11:865–884.

Black, A.L. 1970. Soil water and soil temperature influences on dryland winter wheat. Agron. J. 62:797–801.

----. 1973a. Crop residue, soil water, and soil fertility related to spring wheat production and quality on fallow. Soil Sci. Soc. Am. Proc. 37:754–748.

----. 1973b. Soil property changes as associated with crop residue management in a wheat-fallow rotation. Soil Sci. Soc. Am. Proc. 37:943–946.

----. 1982. Long-term N-P fertilizer and climate influences on morphology and yield components of spring wheat. Agron. J. 74:651–657.

----, and R.H. Ford. 1976. Available water and soil fertility relationships for annual crop-

ping systems. p. 286–290. *In* A. Shaw et al. (ed.) Proc. Regional Saline-Seep Control Symp., Bozeman, MT. 9–11 Dec. 1975. Montana Coop. Ext. Bull. 1132.

----, A.D. Halvorson, L.L. Reitz, and C.A. Reule. 1980. Spring wheat stand and yield losses from applying urea-N fertilizer with the seed. North Dakota Farm Res. 37(3):8–12.

----, and J.F. Power. 1965. Effect of chemical and mechanical fallow methods on moisture storage, wheat yields, and soil erodibility. Soil Sci. Soc. Am. Proc. 29:465–468.

----, and F.H. Siddoway. 1976. Dryland cropping sequences within a tall wheatgrass barrier system. J. Soil Water Conserv. 31:101–105.

----, and ----. 1977a. Hard red and durum spring wheat responses to seeding date and NP-fertilization on fallow. Agron. J. 69:885–888.

----, and ----. 1977b. Winter wheat recropping on dryland as affected by stubble height and nitrogen fertilization. Soil Sci. Soc. Am. J. 41:1186–1190.

Blair, A.W., and A.L. Prince. 1923. Studies on toxic properties of soils. Soil Sci. 15:109–123.

Bond, J.J., and D.E. Umberger. 1979. Technical and economic causes of productivity changes in U.S. wheat production, 1949–76. USDA Tech. Bull. 1598.

----, and W.O. Willis. 1969. Soil water evaporation: Surface residue rate and placement effects. Soil Sci. Soc. Am. Proc. 33:445–448.

----, and ----. 1971. Soil water evaporation: long-term drying as influenced by surface residue and evaporation potential. Soil Sci. Soc. Am. Proc. 35:984–987.

Boswell, F.C., L.R. Nelson, and M.J. Bitzer. 1976. Nitrification inhibitor with fall-applied vs. split nitrogen applications for winter wheat. Agron. J. 68:737–740.

Brawand, H. 1964. Crop residue effect on soil properties and soil moisture conservation in the Blacklands. Texas Res. Found. Bull. 20. Renner.

Brewster, B.D., A.P. Appleby, and R.L. Spinney. 1977. Control of Italian ryegrass and wild oats in winter wheat with HOE 23408. Agron. J. 69:911–913.

Briggs, K.G., and A. Aytenfisu. 1979. The effects of seeding rate, seeding date and location on grain yield, maturity, protein percentage and protein yield of some spring wheats in central Alberta. Can. J. Plant Sci. 59:1139–1145.

----, and ----. 1980. Relationships between morphological characters above the flag leaf node and grain yield in spring wheats. Crop Sci. 20:350–354.

Brown, B. 1982. Idaho fertilizer guide: Irrigated wheat. Current Information Series No. 373. Univ. of Idaho, Moscow.

Brown, P.L., A.L. Black, C.M. Smith, J.W. Enz, and J.M. Caprio. 1981. Soil water guidelines and precipitation probabilities for growing barley and spring wheat in flexible cropping systems — Montana and North Dakota. Mont. State Coop. Ext. Serv. Bull. 356.

Buchholz, D.D. 1983. Soil test interpretations and recommendations handbook. Dep. of Agronomy, Univ. of Missouri.

Burkhead, C.E., J.W. Kirkbride, and L.A. Losleben. 1965. Field and seed crops: Usual planting and harvesting dates by states in principal producing areas. USDA Agric. Handb. 283. U.S. Government Printing Office, Washington, DC.

Burleigh, J.R., R.E. Allan, and O.A. Vogel. 1965. Varietal differences in seedling emergence of winter wheats as influenced by temperature and depth of plants. Agron. J. 57:195–198.

Burwell, R.E., and W.E. Larson. 1969. Infiltration as influenced by tillage induced random roughness and pore space. Soil Sci. Soc. Am. Proc. 33:449–452.

Button, R. 1978. Potassium deficiencies in northeast Saskatchewan. Better Crops Plant Food (Winter) 62:22–23.

Campbell, C.A., W. Nicholaichuk, D.W. McAndrew, G.E. Parker, and J.D. Beaton. 1984. Effect of stubble height and source, rate, time, and method of application of N on yield of spring and winter wheat grown under zero till. *In* Proc. Maximum Wheat Yield Systems Workshop, Denver, CO. 7–9 Mar. 1984. Potash and Phosphate Institute, Atlanta, GA.

Chan, L.M., R.R. Johnson, and C.M. Brown. 1980. Relay intercropping soybeans into winter wheat and spring oats. Agron. J. 72:35–39.

Chapman, S.R., and L.P. Carter (ed.). 1976. Crop production — principles and practices. Cropping systems and resource conservation. W.F. Freeman and Co. Publishers, San Francisco.

Chepil, W.S. 1946. Germination of weed seeds. I. Longevity, periodicity of germination, and vitality of seeds in cultivated soil. Sci. Agric. (Ottowa) 26:307–346.

Christensen, N.W., T.L. Jackson, and R.L. Powelson. 1982. Suppression of take-all root rot and stripe rust diseases of wheat with chloride fertilizer. Proc. 9th Int. Plant Nutr. Colloq., Warwick Univ., England. 22–27 August 1982. 1:111–116 Commonwealth Agric. Bureaux.

----, and R.J. Killorn. 1981. Wheat and barley growth and N fertilizer utilization under sprinkler irrigation. Agron. J. 73:307–312.

----, and V.W. Meints. 1982. Evaluating N fertilizer sources and timing for winter wheat. Agron. J. 74:840–844.

----, R.G. Taylor, T.L. Jackson, and B.L. Mitchell. 1981. Chloride effects on water potentials and yield of winter wheat infected with take-all root rot. Agron. J. 73:1053–1058.

Ciha, A.J. 1983. Seeding rate and seeding date effects on spring seeded small grain cultivars. Agron. J. 75:795–799.

Cope, J.T., Jr. 1981. Effects of 50 years of fertilization with phosphorus and potassium on soil test levels and yields at six locations. Soil Sci. Soc. Am. J. 45:342–347.

Dahnke, W.C. 1983. Soil testing and soil fertility management. p. 75–86. *In* 1984 Crop production guide. North Dakota State Univ., Fargo.

----, and L.J. Swenson. 1983. NDSU-Soil test recommendations. p. 71–74. *In* 1984 Crop production guide. North Dakota State Univ., Fargo.

----, ----, and R.J. Goos. 1983. Choosing a crop yield goal. p. 69–70. *In* 1984 Crop production guide. North Dakota State Univ., Fargo.

Day, A.D., A. Alemu, and E.B. Jackson. 1976. Effect of cultural practices on grain yield and yield components in irrigated wheat. Agron. J. 68:132–134.

----, and S. Intalap. 1970. Some effects of soil moisture stress on the growth of wheat (*Triticum aestivum* L. em. Thell.). Agron. J. 62:27–29.

Deibert, E.J., D.A. Lozotte, and B.R. Bock. 1985. Wheat seed germination as influenced by fertilizer rate, fertilizer source, and spreader type with one-pass pneumatic seeding-fertilizing. North Dakota Farm Res. 42(6):14–20.

Deschenes, J.-M., and J.-P. Dubuc. 1981. Effets de l'humidité du sol, des dates de semis et des mauvaises herbes sur le rendement des céréales. Can. J. Plant Sci. 61:851–857.

Doll, E.C. 1962. Effects of fall-applied nitrogen fertilizer and winter rainfall on yield of wheat. Agron. J. 54:471–473.

----, and R.E. Lucas. 1973. Testing soils for potassium, calcium, and magnesium. p. 133–151. *In* L.M. Walsh and J.D. Beaton (ed.) Soil testing and plant analysis. Soil Science Society of America, Madison, WI.

Donnelly, K.J., and W.E. McMurphy. 1983. Cultural practices for maximizing forage production in wheat. p. 3–22. *In* G.W. Horn (ed.) Proc. Natl. Wheat Pasture Symp., Stillwater, OK. 24–25 October Oklahoma State Univ., Stillwater.

Donohue, S.J., and D.E. Brann. 1984. Optimum N concentration in winter wheat grown in the Coastal Plain region of Virginia. Commun. Soil Sci. Plant Anal. 15:651–661.

Dregne, H.E., and W.O. Willis (ed.) 1983. Dryland agriculture. Agronomy 23.

Edwards, W.M., and W.E. Larson. 1969. Infiltration of water into soils as influenced by surface seal development. Trans. Am. Soc. Agric. Eng. 12:463–465, 470.

Ellis, R. 1979. Influence of soil, liming, magnesium, potassium and nitrogen on magnesium composition of plants. p. 79–92. *In* Grass tetany, American Society of Agronomy, Madison, WI.

Engle, C., F. Entenmann, R. Hermanson, H. Hinman, R. Meyer, and G. Hyde. 1982. No-tillage grain production in the intermediate rainfall area of eastern Washington. Washington State Univ. Ext. Bull. 1038.

Erickson, P.I., M.B. Kirkham, and J.F. Stone. 1979. Growth, water relations, and yield of wheat planted in four row directions. Soil Sci. Soc. Am. J. 43:570–574.

Evans, C.E., and E.J. Kamprath. 1970. Lime response as related to percent Al saturation, solution Al, and organic matter content. Soil Sci. Soc. Am. Proc. 34:893–896.

Evans, L.E., and G.M. Bhatt. 1977. Influence of seed size, protein content and cultivar on early seedling vigor in wheat. Can. J. Plant Sci. 57:929–935.

Fales, S.L., and K. Ohki. 1982. Manganese deficiency and toxicity in wheat: Influence on growth and forage quality of herbage. Agron. J. 74:1070–1073.

Faris, D.G., and R.M. DePauw. 1981. Effect of seeding rate on growth and yield of three spring wheat cultivars. Field Crops Res. 3:289–301.

Fenster, C.R., C.E. Domingo, and O.R. Burnside. 1969. Weed control and plant residue maintenance with various tillage treatments in a wheat-fallow rotation. Agron. J. 61:256–259.

----, and T.M. McCalla. 1970. Tillage practices in western Nebraska with a wheat fallow rotation. Nebr. Agric. Exp. Stn. Bull. 507.

----, H.I. Owens, and R.H. Follett. 1977. Conservation tillage for wheat in the Great Plains. USDA Ext. Ser. PA-1190.

Ferguson, W.S. 1967. Effect of repeated applications of straw on grain yields and on some soil properties. Can. J. Soil Sci. 47:117–121.

Fick, G.N., and C.O. Qualset. 1976. Seedling emergence, coleoptile length, and plant height relationships in crosses of dwarf and standard-height wheats. Euphytica 25:679–684.

Finnerty, D.W., and D.L. Klingman. 1962. Life cycles and control studies of some weed bromegrasses. Weeds 10:40–47.

Fleming, A.L., and C.D. Foy. 1969. Root structure reflects differential aluminum tolerance in wheat varieties. Agron. J. 60:172–176.

Follett, R.H., L.S. Murphy, and R.L. Donahue. 1981. Fertilizers and soil amendments. Prentice-Hall, Englewood Cliffs, NJ.

Fowler, D.B. 1982. Date of seeding, fall growth, and winter survival of winter wheat and rye. Agron. J. 74:1060–1063.

----, and I.A. de la Roche. 1984. Winter wheat production on the north central Canadian Prairies: Protein quality classes. Crop Sci. 24:873–876.

Fox, R.H., and W. Piekielek. 1983. Response of corn to nitrogen fertilizer and the prediction of soil nitrogen availability with chemical tests in Pennsylvania. Pa. State Univ. Bull. 843.

Foy, C.D., and J.C. Brown. 1964. Toxic factors in acid soils. II. Differential aluminum tolerance of plant species. Soil Sci. Soc. Am. Proc. 28:27–32.

----, G.R. Burns, J.C. Brown, and A.L. Fleming. 1965. Differential aluminum tolerance of two wheat varieties associated with induced pH changes around their roots. Soil Sci. Soc. Am. Proc. 29:64–67.

----, R.L. Chaney, and M.C. White. 1978. The physiology of metal toxicity in plants. Annu. Rev. Plant Physiol. 29:511–566.

Foy, G.C., H.N. Lafever, J.W. Schwartz, and A.L. Fleming. 1974. Aluminum tolerance of wheat cultivars related to region of origin. Agron. J. 66:751–757.

Fried, M., and M. Peech. 1946. The comparative effects of lime and gypsum upon plants grown on acid soils. J. Am. Soc. Agron. 38:614–623.

Fryrear, D.W. 1976. Continuous cropping as an alternative to fallow in the southern Great Plains. p. 132–144. *In* Conservation tillage. Great Plains Agric. Counc. Pub. 77. Univ. of Nebraska, Lincoln.

Gallagher, P.J., C.L. Harms, and L.S. Murphy. 1973a. Evaluations of sulfur-coated urea as a source of nitrogen for wheat. Kansas Fert. Res. Rep. Prog. 202:53–54, 62–63.

----, R.E. Lamond, B. Buchholz, D.F. Leikam, B. Hall, W.A. Moore, M. Claassen, G. Ten Eyck, and C.W. Swallow. 1977. Effects of soil and foliar nitrogen applications on wheat yield and grain protein. Kansas Fert. Res. Report Prog. 313:16–17, 39.

----, ----, D.A. Hogan, S.J. Schield, and L.S. Murphy. 1975. Effectiveness of topdressed nitrogen sources for wheat. Kansas Fert. Res. Rep. Prog. 255:28–29.

----, W.A. Moore, R.J. Raney, G. TenEyck, R.E. Lamond, G.A. Raines, and D.F. Leikam. 1976. Nitrogen placement effects on wheat yield and grain protein. Kansas Fert. Res. Rep. Prog. 285:11–14.

----, L.S. Murphy, C.L. Harms, and W.A. Moore. 1973b. Comparisons of effects of nitrogen carriers, rates and time of application on yield and quality of winter wheat. Kansas Fert. Res. Rep. Prog. 202:59–60.

Gallaher, R.H. 1975. All out feed production by multiple cropping. Proc. Feed and Feeding Res. Day. Georgia Exp. Stn., Experiment, GA. 1:29–36.

Gardner, E.H., and N.R. Goetze. 1980. Oregon State University fertilizer guide for winter wheat (non-irrigated — Columbia Plateau). FG 54. Oregon State University Ext. Serv., Corvallis.

----, T.L. Jackson, B.G. Wilcox, L. Fitch, M. Johnson, and V. Pumphrey. 1983. Fertilizer guide: Irrigated wheat (Eastern Oregon — east of Cascades). FG 40. Oregon State Univ. Ext. Serv., Corvallis.

----, and F. Nibler. 1984. Fertilizer response of reduced tillage wheat. Better Crops Plant Food (Summer) 68:25–27.

Gates, L.F. 1975. Influence of sowing dates, soil amendments, and cultivars on wheat spindle streak mosaic in winter wheat. Can. J. Plant Sci. 55:891–895.

Gelderman, R., E. Adams, E. Williamson, and P. Carson. 1977. Fertilizer guide for soil test—computerized recommendations. South Dakota State Univ. Plant Sci. Pamphlet 34.

Gibson, R.C., J.P. Jones, and R.E. McDole. 1980. Comparison of urea and ammonium nitrate for spring application of soft white winter wheat. *In* Proc. 31st Annu. Northwest Fertilizer Conf. Pacific Northwest, Salt Lake City, UT. 15–17 July.

Goel, M.C., W.D. Kemper, R.V. Worstell, and J.A. Bondurant. 1982. Cablegation: III. Field assessment of performance. Trans. Am. Soc. Agric. Eng. 25:1304–1309.

Goldstein, Anne (ed.) 1984. 1983 Irrigation survey. Irrig. J. 33:15–22.

Goos, R.J. 1983. Small grain soil fertility investigations, 1979–1983. North Dakota Farm Res. 41(1):27–29, 33.

----. 1984. Post-harvest evaluation of nitrogen management — a new approach for "selling" soil testing to wheat farmers. J. Agron. Educ. 13:103–106.

----, D.G. Westfall, A.E. Ludwick, and J.E. Goris. 1982. Grain protein content as an indicator of N sufficiency for winter wheat. Agron. J. 74:130–133.

Gravelle, W.D. 1983. Influence of timing of nitrogen application on yield and nutrient uptake of winter wheat (*Triticum aestivum* L.). M.S. thesis. Virginia Polytechnic Institute and State Univ., Blacksburg.

Greb, B.W. 1979. Reducing drought effects on croplands in the west-central Great Plains. USDA Inf. Bull. 420. U.S. Government Printing Office, Washington, DC.

----, D.E. Smika, and A.L. Black. 1970. Water conservation with stubble mulch fallow. J. Soil Water Conserv. 25:58–62.

----, ----, N.P. Wosdauff, and C.J. Whitfield. 1974. Summer fallow in the central Great Plains. p. 51–85. *In* Summer fallow in the western United States. USDA-ARS Conserv. Res. Rep. 17. U.S. Government Printing Office, Washington, DC.

Griffin, G.F., and W.J. Hanna. 1967. Phosphorus fixation and profitable fertilization: 1. Fixation in New Jersey soils. Soil Sci. 103:202–208.

Grunes, D.L. 1959. Effect of nitrogen on the availability of soil and fertilizer phosphorus to plants. Adv. Agron. 11:369–397.

Haas, H.J., W.O. Willis, and J.J. Bond. 1974a. Summer fallow in the northern Great Plains (sping wheat). p. 12–35. *In* Summer fallow in the western United States. USDA-ARS Conserv. Res. Rep. 17. U.S. Government Printing Office, Washington, DC.

----, ----, and ---- (ed.) 1974b. Summer fallow in the western United States. USDA-ARS Conserv. Res. Rep. 17. U.S. Government Printing Office, Washington, DC.

Halvorson, A.D., and A.L. Black. 1985a. Long-term dryland crop responses to residual phosphorus fertilizer. Soil Sci. Soc. Am. J. 49:928–933.

----, and ----. 1985b. Fertilizer phosphorus recovery after seventeen years of dryland cropping. Soil Sci. Soc. Am. J. 49:933–937.

----, ----, F. Sobolik, and N. Riveland. 1976. Proper Management: Key to successful winter wheat recropping in northern Great Plains. North Dakota Farm Res. 33(4):3–9.

----, and P.O. Kresge. 1982. FLEXCROP: A dryland cropping systems model. USDA-ARS Production Res. Rep. 180.

Hammel, J.E., R.I. Papendick, and G.S. Campbell. 1981. Fallow tillage effects on evaporation and seedzone water content in a dry summer climate. Soil Sci. Soc. Am. J. 45:1016–1022.

Hansen, V.E., O.W. Israelsen, and G.E. Stringham. 1979. Irrigation principles and practices. 4th ed. John Wiley and Sons, New York.

Hanson, R.G., S.R. Maledy, R.D. Hoette, N.W. Watchinski, and C.E. Hentes. 1984. Nitrogen source, time of application, and nitrification inhibitor effect on yield of winter wheat. J. Fertilizer Issues 1:54–61.

Hanson, R.L. 1984. Phosphorus transformations of dual nitrogen and phosphorus application. M.S. thesis, Colorado State Univ.

----, and D.G. Westfall. 1983. Phosphorus solubility relationships of common N and P fertilizer injection zones. p. 50–52. *In* Proc. Western Phosphate Conf., Ft. Collins, CO 17–18 Mar. 1983.

Harapiak, J.T., and N.A. Flore. 1984. Pre-plant banding of N and N-P fertilizers: Western Canadian research. p. 43–51. *In* Proc. 35th Annu. Northwest Fertilizer Conf., Pasco, WA. 17–18 July 1984.

Harder, R.W., and W.L. Thiessen. 1971. Sulfur fertilizer improves yield and quality of soft white winter wheat. Univ of Idaho Coop. Ext. Serv. Current Information Series 165.

Hargrove, W.L., D.E. Kissel, and L.B. Fenn. 1977. Field measurements of ammonia volatilization from surface applications of ammonium salts to a calcareous soil. Agron. J. 69:473–476.

----, J.T. Touchton, and J.W. Johnson. 1983. Previous crop influence on fertilizer nitrogen requirements for double-cropped wheat. Agron. J. 75:855–859.

Harms, C.L. 1976. Magnesium effects on wheat forage components in the tetany syndrome. Ph.D. diss. Kansas State Univ. (Diss. Abstr. DOJ 77-16012.)

----, D.A. Hogan, P.J. Gallagher, C.A. Morris, and L.S. Murphy. 1974. Comparative performance of five nitrogen carriers topdressed on wheat. Kansas Fert. Res. Report Prog. 224:49–50.

Hays, W.A. 1982. How systems compare for yield. p. 71–84. *In* W.A. Hays (ed.) Minimum tillage farming. No-Till Farmer, Brookfield, WI.

Herbek, J.A., L.W. Murdock, W.A. Talley, and C.R. Tutt. 1984. Effect of nitrogen on the yield and lodging of some new wheat varieties. *In* 1984 Agron. Res. Rep. Univ. of Kentucky, Lexington.

Hoeft, R.G. 1984. Fertilization of wheat, oats, and barley. *In* 1983–84 Illinois Agron. Handb. Cir. 1208. Univ. of Illinois, Urbana.

Hooker, M.L., S.H. Mohiuddin, and E.T. Kanemasu. 1983. The effect of irrigation timing on yield and yield components of winter wheat. Can. J. Plant Sci. 63:815–823.

Huber, D.M. 1979. Multi-adversity relationships of seeding date as a cultural pest control tactic. p. 77. *In* Proc. 9th Int. Cong. Plant Prot. Washington, DC. 5–11 August. American Phytopathological Society, St. Paul, MN.

----, H.L. Warren, D.W. Nelson, C.Y. Tsai, and G.E. Shaner. 1980. Response of winter wheat to inhibiting nitrification of fall-applied nitrogen. Agron. J. 72:632–637.

Hue, N.V., F. Adams, and C.E. Evans. 1984. Plant available sulfur as measured by soil-solution sulfate and phosphate-extractable sulfate in an ultisol. Agron. J. 76:726–730.

Hutchinson, F.E., and A.S. Hunter. 1970. Exchangeable aluminum levels in two soils as related to lime treatment. Agron. J. 62:702–704.

Isaac, R.A. 1983. Reference soil test methods for the southern region of the United States. Univ. of Georgia Southern Coop. Series Bull. 289, Athens.

Jackson, T.L., A.D. Halvorson, and B.B. Tucker. 1983a. Soil fertility in dryland agriculture. p. 297–332. *In* H.E. Dregne and W.O. Willis (ed.) Dryland Agriculture. Agronomy 23.

----, R.L. Powelson, and N.W. Christensen. 1983b. Combatting take-all root rot of winter wheat in western Oregon. Fact Sheet No. 250. Oregon State Univ. Coop. Ext. Serv., Corvallis.

Jensen, M.E., D.C.N. Robb, and C.E. Franzoy. 1970. Scheduling irrigations using climate-crop-soil data. J. Irrig. Drain. Div. Am. Soc. Civ. Eng. 96:25–38.

----, J.L. Wright, and B.J. Pratt. 1971. Estimating soil moisture depletion from climate, crop and soil data. Trans. Am. Soc. Agric. Eng. 14:954–959.

Johnson, G.V., and B.B. Tucker. 1982. OSU soil test calibrations. Okla. State Univ. Coop. Ext. Serv. Facts 2225.

Johnson, J., J.R. Miller, D. Mengel, G.J. Racz, T. Jackson, B. Segars, A.R. Halvorson, and B. Brown. 1984b. Fall-winter fertilization: Here's what the experts say. Better Crops Plant Food (Fall) 68:12–14.

Johnson, J.W., W.L. Hargrove, J.T. Touchton, and W.T. Yamazaki. 1984a. Influence of N fertilization on wheat milling and baking quality. Crop Sci. 24:904–906.

Johnson, W.C. 1950. Stubble mulch farming on wheatlands of the southern high plains. USDA Cir. 860. U.S. Government Printing Office, Washington, DC.

Johnston, R.A., G.V. Johnson, and B.B. Tucker. 1983. Guidelines for topdressing wheat. Mimeographed report, Dep. of Agronomy, Oklahoma State Univ.

Jose, H.D., and L. Nilsen. 1982. Batch and annual phosphorus fertilizer application for wheat in western Canada. Better Crops Plant Food. (Summer) 66:29–31.

Kamprath, E.J., and M.E. Watson, 1980. Conventional soil and tissue tests for assessing the phosphorus status of soils. p. 433–469. *In* F.E. Khasawneh et al. (ed.) The role of phosphorus in agriculture. American Society of Agronomy, Madison, WI.

Karlen, D.L. 1978. Influence of soil and climatic factors on forage quality indices of grass tetany in ruminants. Ph.D. diss., Kansas State Univ., Manhattan. (Diss. Abstr. DOJ 79-15173.)

Kelley, K.W., M.C. Lundquist, W.A. Moore, R.E. Lamond, B. Hall, D. Buchholz, and L.S. Murphy. 1977. Wheat reponses to P materials, P rates and methods of application. Kans. Fert. Res. Rep. Prog. 313:26–27.

Kemper, W.D., W.H. Heinemann, D.C. Kincaid, and R.V. Worstell. 1981. Cablegation: I. Cable controlled plugs in perforated supply pipes for automatic furrow irrigation. Trans. Am. Soc. Agric. Eng. 24:1526–1532.

Ketata, H., L.H. Edwards, and R.D. Morrison. 1976. Response of three hard red winter wheat cultivars to four planting arrangements. Agron. J. 68:428–429.

Kirkham, M.B. 1982. Orientation of leaves of winter wheat planted in north–south or east–west rows. Agron. J. 74:893–898.

Kissel, D.E., and D.A. Whitney. 1979. Phosphorus placement for wheat. Kans. Coop. Ext. Serv. Ag Facts 40.

----. 1982. Topdress or preplant applications of N can boost winter wheat yields. Solutions 26(2):76–92.

Knapp, W.R., and J.S. Knapp. 1978. Response of winter wheat to date of planting and fall fertilization. Agron. J . 70:1048–1053.

Knudsen, D., G.A. Patterson, and P.F. Pratt. 1982. Lithium, sodium, and potassium. *In* A.L. Page (ed.) Methods of soil analysis. 2nd ed., Part 2. Agronomy 9:225–246.

Koehler, F.E. 1985. Wheat takes up much plant food. Potash and Phosphate Institute Pamphlet.

Kolp, B.J., R.G. Sackett, K.E. Bohnenblust, and G.P. Roehrkasse. 1973. Effect of rate and date of seeding Shoshoni winter wheat on soil moisture depletion. Agron. J. 65:929–930.

Lafever, H.N., L.G. Campbell, and C.D. Foy. 1977. Differential response of wheat cultivars to Al. Agron. J. 69:563–569.

Lamond, R.E. 1978. Effects of nitrogen form, magnesium application, and soil temperature

on grass tetany related components of winter wheat and tall fescue. Ph.D. diss. Kansas State U niv., Manhattan.

----, D.A. Whitney, J.H. Long, and G.R. TenEyck. 1984. Effects of sulphur rates, sources and application methods on wheat. Kansas Fert. Res. Rep. Prog. 462:9–10.

Larson, W.E., and W.R. Gill. 1973. Soil physical parameters for designing new tillage systems. p. 13–22. *In* Proc. Conservation tillage, 28–30 March 1973, Des Moines, IA. Soil Conservation Society of America, Ankeny, IA.

----, R.F. Holt, and C.W. Carlson. 1978. Residues for soil conservation. p. 1–15. *In* W.R. Oschwald (ed.) Crop residue management systems. Spec. Pub. 31. American Society of Agronomy, Madison, WI.

Lathwell, D.J., and W.S. Reid. 1984. Crop response to lime in the northeastern United States. *In* F. Adams (ed.) Soil acidity and liming, 2nd ed. Agronomy 12:305–332.

Leggett, G.E. 1959. Relationship between wheat yield, available moisture and available nitrogen in eastern Washington dry land areas. Wash. Agric. Exp. Stn. Bull. 609.

Leholm, A., and E.H. Vasey. 1983. "CROPPAK", A short run crop enterprise analysis program available on AGNET — A management tool for agriculture. N.D. State Univ. Coop. Ext. Serv. Fargo.

Leikam, D.F., D.E. Kissel, and D.A. Whitney. 1979. Nitrification inhibitor studies. Kansas Fert. Res. Rep. Prog. 372:11–16.

----, K. Winter, D.D. Scott, D.A. Whitney, M. Blocker, and L.S. Murphy. 1978. Effects of methods of N and P application and P rate on winter wheat. Kansas Fert. Res. Report Prog. 343:27–29.

----, L.S. Murphy, D.E. Kissel, D.A. Whitney, and H.C. Moser. 1983. Effects of nitrogen and phosphorus application method and nitrogen source on winter wheat yield and leaf tissue phosphorus. Soil Sci. Soc. Am. J. 47:530–535.

Lewis, W.M., and J.A. Phillips. 1976. Double cropping in eastern United States. p. 41–50. *In* R.I. Papendick et al. (ed.) Multiple cropping. Spec. Pub. 27. American Society of Agronomy, Madison, WI.

Lindstrom, M.J., R.I. Papendick, and F.E. Koehler. 1976. A model to predict winter wheat emergence as affected by soil temperature, water potential, and depth of planting. Agron. J. 68:137–141.

Lindwall, C.W., and D.T. Anderson. 1981. Agronomic evaluation of minimum tillage systems for summer fallow in southern Alberta. Can. J. Plant Sci. 61:247–253.

Liu, S.L., E.C. Varsa, G. Kapusta, and D.N. Mburu. 1984. Effect of etridiazol and nitrapyrin treated N fertilizers on soil mineral N status and wheat yields. Agron. J. 76:265–270.

Longley, T.S. 1984. Basin tillage for irrigated small grain production. Paper No. PNR84-209. PNR Annual Meeting Am. Soc. Agric. Eng., Kennewick, Washington. p. 338–345. *In* Proc. Am. Soc. Civil Engineers, Irrigation and Drainage Division Meetings, 24–26 July. American Society of Civil Engineers, New York.

Lyles, Leon, J.D. Dickerson, and N.F. Schmeidler. 1974. Soil detachment from clods by rainfall: Effects of wind, mulch cover, and initial soil moisture. Trans Am. Soc. Agric. Eng. 17:697–700.

----, L.J. Hagen, and E.L. Skidmore. 1983. Soil conservation: principles of erosion by wind. *In* H.E. Dregne and W.O. Willis (ed.) Dryland agriculture. Agronomy 23:177–188.

----, and N.P. Woodruff. 1962. How moisture and tillage affect soil cloddiness for wind erosion control. Agric. Eng. 43:150–153, 159.

Makarim, A.K., and F.R. Cox. 1983. Evaluation of the need for copper with several soil extractants. Agron. J. 75:493–496.

Marion, G.M., D.M. Hendricks, G.R. Dutt, and W.H. Fuller. 1976. Aluminum and silica solubility in soils. Soil Sci. 121:76–85.

Martens, D.C. 1976. Cause and control of copper deficiency of agronomic crops. International Copper Research Association Project No. 226(A), Final Report. Agronomy Dep., Virginia Polytechnic Institute and State Univ., Blacksburg.

Massee, T.W., and C.G. Painter. 1979. Using yield and protein history from dryland fields

to improve nitrogen fertilizer recommendations. p. 135–141. *In* Proc. 30th Annu. Northwest Fertilizer Conf. Spokane, WA, 17–19 July 1979. Northwest Fertilizer Association.

Mathews, O.R. 1945. Crop residue management in dry-land crop production. J. Am. Soc. Agron. 37:297–306.

McCalla, T.M., and T.J. Army. 1961. Stubble mulch farming. Adv. Agron. 13:125–196.

----, and J.C. Russel. 1943. Nitrate production as affected by grain crop residues on the surface of the soil. Univ. of Nebraska Res. Bull. 131.

McDole, R.E., J.P. Jones, and R.W. Harder. 1978. North Idaho Fertilizer Guide: Wheat. Univ. Idaho Current Information Series 453.

McGuire, C.F., J.R. Sims, F.H. McNeal, and P.L. Brown. 1974. Fertilizing Montana wheats to improve grain yield and milling and baking quality. Mont. Agric. Exp. Stn. Bull. 674.

McKenzie, R.H. 1983. Micronutrient requirements of crops in Alberta. Alberta Agriculture, Agdex 531-1.

Miley, W.N., S.L. Chapman, and J.T. Batchelor. 1982. Fertilizing and liming wheat on sandy and silty soils. Univ. of Arkansas Ext. Pub. EL58.

Miller, M.H., and A.J. Ohlrogge. 1958. Principles of nutrient uptake from fertilizer bands. I. Effect of placement of nitrogen fertilizer on the uptake of band-placed phosphorus at different soil phosphorus levels. Agron. J. 50:95–97.

Moraghan, J.T. 1984. Differential responses of five species to phosphorus and zinc fertilizers. Commun. Soil Sci. Plant Anal. 15(4):437–447.

Mortvedt, J.J. (ed. chair) 1972. Micronutrients in agriculture. Soil Science Society of America, Madison, WI.

Mugwira, L.M., V.T. Sapra, S.U. Patel, and M.A. Choudry. 1981. Aluminum tolerance of triticale and wheat cultivars developed in different regions. Agron. J. 73:470–475.

Murdock, L.W. 1984. Effect of nitrification inhibitors on wheat yields in Kentucky. Abstr. tech. papers, 1984 Annu. Meeting, Southern Branch of Am. Soc. of Agron., Nashville, TN.

Murphy, L.S. 1979. MAP, DAP, Poly and Rock. North Central Extension-Industry Soil Fertility Workshop, St. Louis, MO. Oct. 31–Nov. 1.

----. 1987. Agronomic characteristics of fluids (fertilizers). *In* D.A. Palgrave (ed.) fluid fertilizer technology. Marcel Dekker, New York. (In press.)

Musick, J.T., and D.A. Dusek. 1980. Planting date and water deficit effects on development and yield of irrigated winter wheat. Agron. J. 72:45–52.

Norwood, C.A. 1984. Research on wheat-fallow and wheat-sorghum-fallow. p. 14–17. *In* Jim Stiegler (ed.) Proc. Conserv. Tillage Conf.: Crop Clinics. Ext. Pub., Oklahoma State Univ., Stillwater.

Ohki, K. 1984. Manganese deficiency and toxicity effects on growth, development and nutrient composition in wheat. Agron. J. 76:213–218.

Olsen, S.R., C.V. Cole, F.S. Watanabe, and L.R. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. 939. U.S. Government Printing Office, Washington, DC.

Olson, R.A., A.F. Dreier, G.W. Lowrey, and A.D. Flowerday. 1956. Availability of phosphate carriers to small grains and subsequent clover in relation to: I. Nature of soil and method of placement. Agron. J. 48:106–111.

Oplinger, E.S., and D.W. Wiersma. 1984. Intensive wheat management. Univ. of Wisconsin–Madison Dep. of Agronomy Field Crops Bull. 26.4.

Oveson, M.M. 1966. Conservation of soil nitrogen in a wheat-summer fallow farming practice. Agron. J. 58:444–447.

Pairintra, C. 1973. Influence of NH_3 from ammonium phosphate fertilizers on germination, seedling growth, and small plant yield of wheat (*Triticum aestivum* L.) Ph.D. diss. Montana State Univ., Bozeman (Diss Abstr. 73:27490).

Papendick, R.I., M.J. Lindstrom, and V.L. Cochran. 1973. Soil mulch effects on seedbed

temperature and water during fallow in eastern Washington. Soil Sci. Soc. Am. Proc. 37:307–314.

Parsons, B.C., and F.E. Koehler. 1984. Fertilizer use by spring wheat as affected by placement. p. 101–107. *In* Proc. 35th Annu. Northwest Fertilizer Conf., Pasco, WA. 17–18 July 1984.

Pearson, R.W., and F. Adams (ed.) 1967. Soil acidity and liming. Agronomy 12.

Peck, T.R., L.T. Kurtz, and H.L.S. Tandon. 1971. Changes in Bray P, soil phosphorus test values resulting from applications of phosphorus fertilizer. Soil Sci. Soc. Am. Proc. 35:595–598.

Penas, E.J., and D.H. Sander. 1982. Dual placement of nitrogen and phosphorus for winter wheat. p. 7.1–7.2. *In* Soil Science Research Report. Dep. of Agronomy, Univ. of Nebraska, Lincoln.

Peterson, G.A., D.H. Sander, P.H. Grabouski, and M.L. Hooker. 1981. A new look at row and broadcast phosphate recommendations for winter wheat. Agron. J. 73:13–17.

----, ----, ----, and ----. 1982. Efficient use of phosphorus on winter wheat. Better Crops Plant Food. (Spring) 62:3–5.

Petrie, S.E., and B. Brown. 1983. Effects of N and Cl fertilizers on yield of cereals infected with root rot. p. 57–63. *In* Proc. 34th Annu. Northwest Fertilizer Conf., Portland, OR. 11–13 July 1983.

Pierre, W.H. 1933. Determination of equivalent acidity and basicity of fertilizers. Ind. Eng. Chem. Anal. Ed. 5:229–234.

----, and W.L. Banwart. 1973. Excess-base and excess-base/nitrogen ratio of various crop species and parts of plants. Agron. J. 65:91–96.

----, J. Meisinger, and J.R. Birchett. 1970. Cation-anion balance in crops as a factor in determining the effect of nitrogen fertilizers on soil acidity. Agron. J. 62:106–112.

Potash and Phosphate Institute Staff. 1985. Soil test summaries for P and K. Better Crops Plant Food. (Spring) 69:16–17.

Power, J.F., T.S. Aasheim, and G.P. Hartman. 1958. Spring wheat production and soil and water conservation as influenced by methods of summer fallowing on a chestnut soil in northeastern Montana. Soil Sci. Soc. Am. Proc. 22:460–463.

----, and J.O. Legg. 1978. Effect of crop residues on soil chemical environment and nutrient availability. p. 85–100. *In* W.R. Oschwald (ed.) Crop Residue Management Systems. Spec. Pub. 31. American Society of Agronomy, Madison, WI.

Powers, W.L. G.W. Wallingford, and L.S. Murphy. 1975. Formulas for applying organic wastes to land. J. Soil Water Conserv. 30:286–289.

Prihar, S.S., K.L. Khera, K.S. Sandhu, and B.S. Sandhu. 1976. Comparison of irrigation schedules based on pan evaporation and growth stages in winter wheat. Agron. J. 68:650–653.

Pumphrey, F.V., and P.E. Rasmussen. 1982. Winter wheat fertilization in the northeast intermountain region of Oregon. Oregon State Univ. Agric. Exp. Stn. Circ. 691.

Puri, Y.P., and C.O. Qualset. 1978. Effect of seed size and seeding rate on yield and other characteristics of durum wheat. Phyton 36:41–51.

Putnam, A.R., and W.B. Duke. 1978. Allelopathy in agroecosystems. Annu. Rev. Phytopathol. 16:431–451.

Rasmussen, P.E., and R.R. Allmaras. 1985. Sulfur fertilization effects on winter wheat yield and extractable sulfur in a semi-arid soils. Agron. J. 78:421–425.

----, and P.O. Kresge. 1986. Plant response to sulfur in the Western U.S. *In* Sulfur in agriculture. Agronomy 27:357–374.

Read, D.W.L., E.D. Spratt, L.D. Bailey, and F.G. Warder. 1977. Residual effects of phosphorus fertilizer. I. For wheat grown on four chernozemic soil types in Saskatchewan and Manitoba. Can. J. Soil Sci. 57:255–262.

----, and F.G. Warder. 1982. Wheat and barley responses to rates of seeding and fertilizer in southwestern Saskatchewan. Agron. J. 74:33–36.

Reitz, L.P. 1976. Wheat in the United States. USDA Agric. Info. Bull. 386. U.S. Government Printing Office, Washington, DC.

Renard, K.G., and G.R. Foster. 1983. Soil Conservation: Principles of erosion by water. *In* H.E. Dregne and W.O. Willis (ed.) Dryland agriculture. Agronomy 23:155–176.

Rice, E.L. 1974. Allelopathy. Academic Press, New York.

Rickman, R.W., B.L. Klepper, and C.M. Peterson. 1983. Time distributions for describing appearance of specific culms of winter wheat. Agron. J. 75:551–556.

Robertson, J.A. 1982. Fertilizer placement. Alberta Agriculture. Agdex 542–5.

Robins, J.S., and C.E. Domingo. 1962. Moisture and nitrogen effects on irrigated spring wheat. Agron. J. 54:135–138.

Rogers, H.T., D.L. Thurlow, and G.A. Buchanan. 1971. Cropping systems and other cultural practices. *In* Soybean production — recent research findings. Auburn Univ. Agric. Exp. Stn. Bull. 413:31–38.

Roth, G.W., H.G. Marshall, O.E. Hatley, and R.R. Hill, Jr. 1984. Effect of management practices on grain yield, test weight, and lodging of soft red winter wheat. Agron. J. 76:379–383.

Russel, J.C. 1976. Some historical aspects of stubble mulch tillage. p. 1–12. *In* Conservation tillage. Great Plains Agric. Counc. Pub. 77. Univ. of Nebraska, Lincoln.

Rydrych, D.J. 1974. Competition between winter wheat and downy brome. Weed Sci. 22:211–214.

Sabbe, W.E. 1978. Nitrogen fertilization of wheat growing on Sharkey clay. Arkansas Farm Res. (November–December issue).

Salter, P.J., and J.E. Goode. 1967. Crop responses to water at different stages of growth. Research Review no. 2. Commonwealth Agric. Bur., Farnham Royal, Bucks, England.

Sanford, J.E., D.L. Myhre, and N.C. Meruine. 1973. Double cropping systems involving no-tillage and conventional tillage. Agron. J. 65:978–982.

Sanmaneechai, M., F.E. Koehler, and S. Roberts. 1984. Nitrogen fertilization practices for sequential cropping of wheat, turnips, and sweet corn. Soil Sci. Soc. Am. J. 48:81–86.

Schaff, B.E., and E.O. Skogley. 1982. Soil profile and site characteristics related to winter wheat response to potassium fertilizers. Soil Sci. Soc. Am. J. 46:1207–1211.

Schmehl, W.R., M. Peech, and R. Bradfield. 1950. Causes of poor growth of plants on acid soils and beneficial effects of liming. Soil Sci. 70:393–410.

Schneider, A.D., J.T. Musick, and D.A. Dusek. 1969. Efficient wheat irrigation with limited water. Trans. Am. Soc. Agric. Eng. 12:23–26.

Schneider, R.P., B.E. Johnson, and F. Sobolik. 1978. Soil management research and saline seep control. p. 211–214. *In* 1979 North Dakota crop production guide. North Dakota State Univ., Fargo.

Segars, W.I. 1982. Small grain fertilization. p. 8–10. *In* R.D. Lee et al. (ed.). Small grain production in Georgia. Univ. of Georgia Misc. Pub. 134.

Sharpe, R.R., J.T. Touchton, F.C. Boswell, and W.L. Hargrove. 1984. Effect of applied and residual P on double-cropped wheat and soybean under conservation tillage management. Agron. J. 76:31–35.

Siddoway, F.H. 1963. Effects of cropping and tillage methods on dry aggregate soil structure. Soil Sci. Soc. Am. Proc. 27:452–454.

Singer, M.J., Matsuda Yutaka, and John Blackard. 1981. Effect of mulch rate on soil loss by raindrop splash. Soil Sci. Soc. Am. J. 45:107–110.

Singh, S.D. 1981. Moisture-sensitive growth stages of dwarf wheat and optimal sequencing of evapotranspiration deficits. Agron. J. 73:387–391.

Skidmore, E.L., and F.H. Siddoway. 1978. Crop residue requirements to control erosion. p. 17–33. *In* W.R. Oschwald (ed.) Crop residue management systems. Spec. Pub. 31. American Society of Agronomy, Madison, WI.

Skogley, E.O. 1976. Potassium in Montana soils and crop requirements. Mont. Agric. Exp. Stn. Res. Rep. 88.

----, and V.A. Haby. 1981. Predicting crop responses on high-potassium soils of frigid temperature and ustic moisture regimes. Soil Sci. Soc. Am. J. 45:533–536.

Smid, A.E., and R.C. Jenkinson. 1979. Effect of rate and date of seeding on yield and yield

components of two winter wheat cultivars grown in Ontario. Can. J. Plant Sci. 59:939–943.

Smika, D.E. 1970. Summer fallow for dryland winter wheat in the semi-arid Great Plains. Agron. J. 62:15–17.

———. 1976a. Mechanical tillage for conservation fallow in the semiarid central Great Plains. *In* Conservation tillage. Great Plains Agric. Counc. Pub. 77. Univ. of Nebraska, Lincoln.

———. 1976b. Seed zone soil water conditions with reduced tillage in the semiarid central Great Plains. p. 1–6. *In* Proc. 7th Conf. Int. Soil Tillage Res. Organ., 15–18 June 1976, Uppsala. Dep. Soil Sci. Agric. College, Uppsala, Sweden.

———, and B.W. Greb. 1975. Nonerodible aggregates and concentration of fats, waxes, and oils in soils as related to wheat straw mulch. Soil Sci. Soc. Am. Proc. 39:104–107.

———, A.L. Black, and B.W. Greb. 1969. Soil nitrate, soil water, and grain yields in a wheat-fallow rotation in the Great Plains as influenced by straw mulch. Agron. J. 61:785–787.

———, and C.J. Whitfield. 1966. Effect of standing wheat stubble on storage of winter precipitation. J. Soil Water Conserv. 21:138–141.

Smith, C.M., C. Pairintra, and E.O. Skogley. 1973. Comparisons of different ammonium phosphates — influence on germination, seedling injury, and yield of wheat. p. 115–121. *In* Proc. 24th Annu. Pacific Northwest Fertilizer Conf., Pendleton, OR. Northwest Plant Food Association.

Stanford, G. 1982. Assessment of soil nitrogen availability. *In* F.J. Stevenson (ed.) Nitrogen in agricultural soils. Agronomy 22:561–720.

———, O.L. Bennett, and J.F. Power. 1973. Conservation tillage practices and nutrient availability. p. 54–62. *In* Conservation tillage. Soil Conservation Society of America, Ankeny, IA.

Staple, W.J., J.J. Lehane, and A. Wenhardt. 1960. Conservation of soil moisture from fall and winter precipitation. Can. J. Soil Sci. 40:80–88.

Stoa, T.E., and J.C. Zubriski. 1969. Crop rotation, crop management and soil fertility studies on Fargo clay. North Dakota Exp. Stn. Res. Rep. 20.

Stoskopf, N.C. 1967. Yield performance of upright-leaved selections of winter wheat in narrow row spacings. Can. J. Plant Sci. 47:597–601.

Taylor, H.M. 1967. Effects of tillage-induced soil environmental changes on root growth. p. 15–18, 25. *In* Tillage for greater crop production, 11–12 December 1967, Detroit, MI. American Society Agricultural Engineering Pub. PROC-168. St. Joseph, MI.

Taylor, R.G., T.L. Jackson, R.L. Powelson, and N.W. Christensen. 1983. Chloride, nitrogen form, lime, and planting date effects on take-all root rot of winter wheat. Plant Dis. 67:1116–1120.

Thom, W.O., M.H. Bitzer, and K.L. Wells. 1981. Nitrogen fertilization of wheat. Univ. of Kentucky Agron. Dep. Pub. AGR-87.

Thompson, C.A. 1975. Fertilizing dryland wheat. Kansas Agric. Exp. Stn. Bull. 590.

Tomar, J.S., and R.J. Soper. 1981. Fate of tagged urea-N in the field with different methods of N and organic matter placement. Agron. J. 73:991–995.

Torres, J.L., and G.M. Paulsen. 1982. Increasing seed protein content enhances seedling emergence and vigor in wheat. J. Plant Nutr. 5:1133–1140.

Touchton, J.T., J.W. Johnson, and B.M. Cunfer. 1980. The relationship between phosphorus and copper concentration in wheat. Commun. Soil Sci. Plant Anal. 11:1051–1066.

Unger, P.W. 1968. Soil organic matter and nitrogen changes during 24 years of dryland wheat tillage and cropping practices. Soil Sci. Soc. Am. Proc. 32:427–429.

———. 1972. Dryland winter wheat and grain sorghum cropping systems — northern high plains of Texas. Tex. Agric. Exp. Stn. Bull. 1126.

———. 1982. Surface soil physical properties after 36 years of cropping to winter wheat. Soil Sci. Soc. Am. J. 46:796–801.

———, and A.F. Wiese. 1979. Managing irrigated winter wheat residues for water storage and subsequent dryland grain sorghum production. Soil Sci. Soc. Am. J. 43:582–588.

U.S. Dept. of Commerce, Bureau of the Census. 1964. 1964 Census of Agriculture — United States. U.S. Government Printing Office, Washington, DC.

----. 1974. 1974 Census of Agriculture — United States. U.S. Government Printing Office, Washington, DC.

----. 1982. 1982 Census of Agriculture — United States. U.S. Government Printing Office, Washington, DC.

U.S. Salinity Laboratory Staff. 1954. Diagnosis and improvement of saline and alkali soils. USDA Handb. 60. U.S. Government Printing Office, Washington, DC.

University of Saskatchewan. 1981. Guide to farm practice in Saskatchewan. Univ. of Saskatchewan Division of Extension and Community Relations, Saskatoon.

Unruh, L.G., and D.A. Whitney. 1984. Varying aluminum tolerance in wheat grown in south central Kansas. 1984. Kansas Fert. Res. Rep. Prog. 462:14–16.

Vander Vorst, P.B., G.A. Wicks, and O.C. Burnside. 1983. Weed control in a winter wheat-corn-ecofarming rotation. Agron. J. 75:507–511.

Varvel, G.E. 1982. The effects of anhydrous ammonia at planting time on spring wheat and barley. Agron. J. 74:1081–1083.

----, and J. Grava. 1983. Copper for organic soils. Minnesota Agric. Ext. Serv. Folder 347.

Wagar, B.I., and J.W.B. Stewart. 1984. Maximum yields of spring wheat and P fertilization practices. Proc. Maximum Wheat Yield Systems Workshop, Denver, CO. 7–9 March 1984. Potash and Phosphate Institute, Atlanta, GA.

Walker, D.W. 1978. Potassium fertilization in central Alberta. Better Crops Plant Food (Summer) 62:13–15.

Wallace, S.U., and I.C. Anderson. 1984. Aluminum toxicity and DNA synthesis in wheat roots. Agron. J. 76:5–8.

Wallingford, G.W., L.S. Murphy, W.L. Powers, and H.L. Manges. 1975. Disposal of beef-feedlot manure: Effects of residual and yearly applications on corn and soil chemical properties. J. Environ. Qual. 4:526–531.

Webb, B.B., B.B. Tucker, and R.S. Westermann. 1980. The Magruder plots: Taming the prairies through research. Okla. Agric. Exp. Stn. Bull. B-750.

Welch, L.F., P.E. Johnson, J.W. Pendleton, and L.B. Miller. 1966. Efficiency of fall- versus spring-applied nitrogen for winter wheat. Agron. J. 58:271–274.

Westerman, R.L. 1981. Factors affecting soil acidity. Solutions 25(3):64–81.

White, R.P. 1970. Effects of lime upon soil and plant manganese levels in acid soil. Soil Sci. Soc. Am. Proc. 34:624–629.

Whitney, D.A. 1979. Soil test interpretations and fertilizer recommendations. Kans. Coop. Ext. Serv. Circ. 509.

Wicks, G.A., and D.E. Smika. 1973. Chemical fallow in a winter wheat–fallow rotation. Weed Sci. 21:97–102.

Willey, R.W., and S.B. Heath. 1969. The quantitative relationships between plant population and crop yield. Adv. Agron. 21:281–321.

Willis, W.O. 1976. Dryland agriculture. p. 78–80. *In* R.E. Moreng (ed.) Western resource conference on food production and resources in the West, 15–16 July 1976. Fort Collins, CO.

----, and J.J. Bond. 1971. Soil water evaporation: Reduction by simulated tillage. Soil Sci. Soc. Am. Proc. 35:526–529.

Woodruff, N.P., L. Lyles, F.H. Siddoway, and D.W. Fryrear. 1977. How to control wind erosion. Rev. ed. USDA Agric. Info. Bull. 354. U.S. Government Printing Office, Washington, DC.

Wright, J.L. 1982. New evapotranspiration crop coefficients. J. Irrig. Drain. Div., Am. Soc. Civ. Eng. 108:57–74.

Wright, K.E. 1948. Internal precipitation of phosphorus in relation to aluminum toxicity. Plant Physiol. 18:708–712.

Younts, S.E. 1964. Response of wheat to rates, dates of application and sources of copper and to other micronutrients. Agron. J. 56:266–269.

Zimdahl, R.L. 1980. Weed-crop competition: A review. Int. Plant Prot. Center, Oregon State Univ., Corvallis.

Zingg, A.W., and C.J. Whitfield. 1957. A summary of research experiences with stubble-mulch farming in the Western states. USDA Tech. Bull. 1166. U.S. Government Printing Office, Washington, DC.

7 Wheat Breeding

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7 Wheat Breeding

D. R. Knott, ***coordinator***

In planning the Wheat Breeding chapter for this second edition, we decided there was little purpose in covering the routine breeding methods for self-pollinated crops that are described in plant breeding texts. Instead, our emphasis is on specific applications of procedures to wheat (*Triticum aestivum* L. em. Thell.). The first section covers procedures that can be used in a normal wheat breeding program, particularly those that are still controversial or are evolving. Following this, several special topics related to wheat breeding are discussed—mutation breeding, hybrid wheat, interspecific and intergeneric hybrids, the transfer of alien genes to wheat, and novel approaches to wheat breeding, including the induction of haploids from pollen, somatic tissue culture, and N_2 fixation.

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7A The Application of Breeding Procedures to Wheat

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In the first edition of this monograph, Heyne and Smith (1967) emphasized the balance between art and science in wheat breeding. Perhaps one of the greatest changes since then as been the increasing emphasis on science at all stages in a breeding program. That is not to say that the art is no longer important, particularly when visual selection is being done; nevertheless, the breeder now has an armory of techniques to draw upon.

7A–1 CHOOSING PARENTS

In a breeding program the first step is to choose the parents. Bailey and Comstock (1976) used computer simulation to show that in self-fertilizing species the probability of selecting a line better than either parent is higher if both parents are equally good, (as opposed to one being better than the other). Busch et al. (1974) came to the same conclusion, based on tests with 28 wheat crosses. Clearly the good parents must be sufficiently different genetically so that transgressive segregation can occur in their crosses. This was the case in Busch et al.'s study—the genetic variability was similar in high × high and high × low crosses.

7A–2 EARLY GENERATION SELECTION AND TESTING

Early in his program a wheat breeder has to decide how much selection to do among crosses, and on what basis. Yield tests on early generations of crosses have given conflicting results. For example, Harrington (1940) reported that yield tests on F_2 and F_3 bulks of crosses gave

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a good indication of the potential yield of F_6 and F_7 lines. Cregan and Busch (1977) found that an F_2 bulk gave the best prediction of the yield of F_5 lines from a cross but that midparental values were also useful. Nass (1979) suggested the use of midparental, F_1 and F_2 yields. However, Fowler and Heyne (1955) found that generation-to-generation and year-to-year inconsistencies were large, and early-generation bulk hybrid tests were of no value in predicting yield of selections. In any case, simple bulk hybrid tests measure only the average yield of a cross and give no indication of variability within the cross.

Snape (1982) demonstrated that the frequency of transgressive segregants for yield and yield components can be predicted from a complicated set of early-generation tests. However, most breeders are not willing to spend the time and effort required for extensive early-generation testing, particularly since the midparental yields are of some value in selecting crosses. Breeders may eliminate whole crosses in the F_1 or F_2 generation based on visual observation, and certainly the appearance of a cross will often determine the number of selections taken from it.

The value of selection among plants and among families in early generations is controversial. Shebeski (1967) and Sneep (1977) pointed out that in an F_2 population the frequency of plants carrying all of the favorable alleles desired by a wheat breeder is extremely low, and that it decreases rapidly with increasing generations. Ideally, selection should start in the F_2 generation. However, breeders generally agree that F_2 plant yield has low heritability and selection is relatively ineffective (McGinnis and Shebeski, 1968; Knott, 1972; DePauw and Shebeski, 1973; McVetty and Evans, 1980). While correlations between the yields of F_2 plants and the yields of generations derived from them are often significant, the values are sufficiently low to make it doubtful that harvesting, threshing, and weighing the seed from individual plants is worthwhile. Not only is there a problem of a large environmental variance among F_2 plants, but also genotype $\times$ environment (years) interactions reduce the realized heritability.

Visual selection among plants and families for characters with reasonable heritability, such as height, days to maturity, and strength of straw, is known to be effective.

Several authors have attempted to improve selection among F_2 plants by reducing the environmental variability. Skorda (1973) accurately spaced seeds 5-cm apart in rows 27.5-cm apart, and used blocks to further reduce environmental variability. Over all selections, the correlations between F_2 and F_3 yields were high (0.848** for one cross and 0.871** for a second). (Here and elsewhere, the single and double asterisks indicate a significance at the 0.05 and 0.01 levels of probability, respectively.) Fasoulas (1973) designed a honeycomb planting system for reducing the variation among F_2 plants by eliminating interplant competition and comparing only adjacent plants. Mitchell et al. (1982) found in three durum wheat (*Triticum turgidum* L.) crosses that heritability for yield of F_2 plants grown in a

honeycomb system was only 0.13 to 0.17. McVetty and Evans (1980) grew two lots of F_2 plants of three spring wheat crosses with wide spacing, one lot under stress and one stress-free. The correlations between characters of F_2 plants and F_4 bulks derived from them were generally low, and the efficiency of selection was not improved by growing the F_2 plants under stress-free conditions. Bos (1983) has pointed out that selection under spaced planting is indirect selection for the character under commercial conditions and will be effective only if there is a correlated response. Any system that requires considerable hand labor will have to be highly efficient in order to be attractive to breeders.

Since single plant selection for yield appears to be relatively ineffective, both Shebeski (1967) and Sneep (1977) recommended the use of F_3 yield tests to identify the best F_3 families. Several authors have looked at the value of early generation yield testing of families or lines. DePauw and Shebeski (1973) tested F_3 families in single plots with every third plot planted to a control. When yields were expressed as a percent of the adjacent controls, moderate correlations were obtained between F_3 and F_4 (0.59**), and F_3 and F_5 (0.56*) yields. Knott and Kumar (1975) and Knott (1979) obtained significant correlations between the yield of F_3 families and of F_5 lines derived from them (0.29** and 0.14** in two crosses), but concluded that selection based on F_3 yield tests had limited effect. O'Brien et al. (1978) found that selection based on a three-replicate yield test was effective in only two of four crosses tested. Seitzer and Evans (1978) determined that dominance was the largest component of yield in early generations and that this confounded early generation yield tests. Thakare and Qualset (1978) evaluated single plant and family selection in the F_3 generation and recommended selection among plants within selected families as the most appropriate procedure.

The degree of correlation between yields in F_3 and later generations depends to a considerable extent on year-to-year environmental variation and the resulting genotype $\times$ environment interaction. Thus, although significant correlations of moderate size are often obtained, it is questionable whether the results justify the effort involved. There is the added difficulty that selected families will almost certainly be segregating for many genes. Thus, further selection and yield testing is required in later generations. These problems have led wheat breeders to consider the rapid production of homozygotes by procedures such as single seed descent and anther culture, and the concentration of yield testing on such material. Procedures of this type emphasize the development of lines that are better than the parents, rather than attempting to identify the best possible segregate from a cross.

7A–3 POPULATION IMPROVEMENT

Population improvement has become a standard breeding procedure in cross-pollinated crops such as maize, and has been responsible for

many of the advances made in recent years. This procedure has developed more slowly in self-pollinated crops because of the greater difficulty in making substantial numbers of crosses. Moreover, the fact that the desired end product in a self-pollinated crop is an inbred line, not a heterozygous or heterogeneous population, may have reduced breeders' interest. Nevertheless, there has been increasing interest in recurrent selection and population improvement in wheat as a method of developing better source populations for breeding. In a sense, wheat breeders have used a form of recurrent selection for many years. It is common practice in a breeding program to select lines that are outstanding in some character or characters and to recycle them as parents in new crosses.

Several studies in wheat have shown that procedures involving selection in early generations and intercrossing selected plants or families, can be effective for various characters for several cycles. Byrne and Rasmusson (1974) successfully used three cycles of F_2 and F_3 selection for ^{89}Sr content in wheat grain. Selection for ^{89}Sr content resulted in similar changes in Ca content. Correlated responses occurred in the content of other nutrients in the leaves and stems, but often the changes were in the opposite direction to the changes in ^{89}Sr. Avery et al. (1982) were able to select for early heading in winter wheat through three cycles of intermating selected $S_0(=F_1)$ plants. The largest change occurred in cycle 1, suggesting that selection acted on major genes in cycle 1 and on minor genes in cycles 2 and 3. Busch and Kofoid (1982) used four cycles of recurrent selection among $S_1(=F_2)$ plants to improve kernel weight in spring wheat. The number of kernels per spike declined but yield was unchanged. McNeal et al. (1978) evaluated 2000 cultivars from the World Wheat Collection for protein content, and selected nine high protein, hard red spring wheats, plus 'Centana' and 'MT6618', as parents in a recurrent selection program. Selection for high and low protein was effective through two cycles. Increasing protein tended to reduce yield but progress was made in protein yield (grams per row). Loffler et al. (1983) were also successful in increasing protein content by two cycles of recurrent selection among F_3 lines. Although grain yield was reduced, several lines with increased protein content and above average yield were obtained. However, the authors suggest that some concurrent yield selection will be necessary.

Clearly recurrent selection can be used in wheat and the amount of crossing is not prohibitive. The resulting populations can be used either as sources of parents carrying particular characters or as normal breeding populations.

Several procedures have been proposed to improve recurrent selection. Gilmore (1964) suggested ways of using either cytoplasmic or genetic male sterility in a reciprocal recurrent selection program in cereals. Similarly, Sorrells and Fritz (1982) have pointed out the advantage of using a dominant male sterile gene. Bailey and Comstock (1976) suggested that the probability of obtaining superior genotypes from a cross could be

increased by a new cycle of crossing involving at least four lines selected from the cross.

Several authors have suggested the use of random intermating of F_1 or F_2 plants as a way of breaking up linkage blocks and increasing genetic variability prior to selection. Jensen (1970) proposed a diallel selective mating system which involves crossing a group of parents, intercrossing the F_1s, selecting among the new F_1s and F_2s, and intermating the selected plants. Several cycles of selection and intermating are possible. Altman and Busch (1984) tested the intermating of F_1 plants in three populations and concluded that the procedure resulted in insufficient useful recombination to justify its use.

7A–4 RAPID PRODUCTION OF INBRED LINES

Because of the problems with selection in early generations, particularly for yield, wheat breeders have shown considerable interest in rapid methods of producing inbred lines. Effort can then be concentrated on testing inbred lines rather than on producing them. Two methods of speeding the production of inbred lines have been proposed: (i) single seed descent, and (ii) the production of haploid plants either by wide crosses or anther culture, followed by chromosome doubling. The latter is discussed in a later section.

In the single seed descent (SSD) method, a single seed is taken from each plant, usually starting with the F_2 generation, and the seeds are grown out to produce the next generation. The F_2 plants may be a random sample or they may have undergone selection for characters that have a reasonable level of heritability. The objective in the SSD method is to substantially reduce the amount of material being grown in early generations and to speed up the generation advance. Crosses can be advanced for any number of generations by SSD. In the final generation the plants are spaced to provide sufficient seed to begin the testing of the inbred lines. Since a number of plants will be lost in each generation, allowance must be made for the losses in determining the number of F_2 plants with which to begin.

Several authors have grown SSD populations under crowded conditions in sand with limited nutrients (Grafius, 1965; Tee and Qualset, 1975). The procedure results in small plants which mature quickly but produce only a few seeds or sometimes none. In oat (*Avena sativa* L.), Cisar et al. (1982) found no evidence that the elimination of plants by competition was nonrandom.

Snape and Riggs (1975) looked at the genetic consequences of single seed descent. For various genetic situations, even though the F_2 distributions differed greatly, the distributions of random F_6 lines were fairly similar. They noted that pedigree selection has an advantage over an SSD system, if selection is effective. Knott and Kumar (1975) concluded that

although selection based on the yield of F_3 families had some effect, it was not sufficient to justify the extra labor compared to an SSD procedure.

Thus, the evidence is clear that SSD is a useful procedure, particularly if heritability is low so that early generation selection is ineffective. Newer methods that result in doubled haploids have the potential to speed up generation advance even more. Jinks and Pooni (1981) showed that unless linkage is involved, the expectations are the same for SSD and doubled haploid lines.

7A–5 PLANT ARCHITECTURE

Donald (1962, 1968) stimulated interest in the architecture of crop plants and also focused attention on biological yield and the harvest index (HI = grain yield/aboveground biological yield). Much of the recent increase in yield in wheat has resulted from reduction in height and increases in HI. However, now that HI appears to be approaching a maximum, it may be necessary to increase biological yield while maintaining HI, if further progress it to be made.

Some authors have suggested selecting for HI to improve yield. However, measuring HI involves more work than just measuring yield alone. Since the correlation between HI and yield varies in different crosses and different environments (see Donald and Hamblin, 1976; Allan, 1983), it will be useful as a selection tool only if it has a considerably higher heritability than yield itself.

Selection for HI may have two advantages over selection for yield. First, it measures the plant's ability to partition the photosynthate so that more is distributed to the grain and, therefore, measures one aspect of physiological efficiency rather than just yield. Second, although grain yield of individual spaced plants may have little correlation with yield in solid stands, HI in spaced plants shows a higher correlation with yield in solid stands (Symes, 1972; Fisher and Kertesz, 1976). Breeders often grow spaced plants in early generations. Nass (1980) demonstrated that selection for HI in F_2 plants was successful in increasing yield of F_2-derived F_4 bulks; in his study he used two plant densities and found that coefficients of variation were lower and selection more efficient at the higher density. The question of whether selection for HI is sufficiently better than selection for yield to justify the extra work remains to be established.

Relatively limited work has been done on the architecture of the wheat plant and its relationship to yield. Donald (1968) suggested that the ideal wheat ideotype should have short, strong stems; a few small, erect leaves; a large, erect ear; awns; and a single culm. The advantage of short, strong stems is clear. Tanner et al. (1966) found that wheat, oat, and barley lines with narrow, upright leaves gave the highest yield. However, Carvalho and Qualset (1978) compared erect- and nonerect-leaved segregates from wheat crosses and found no significant differences in yield. Austin et al. (1976) compared an erect- and a lax-leaved winter

wheat, and found that the erect type had greater CO_2 fixation during grain filling, slower senescence, and a slightly higher leaf area index, but showed less translocation of dry matter from the stems.

7A–6 TESTING PROCEDURES

Genotype × environment interactions provide a constant challenge to wheat breeders. A frequent problem in a testing program is to determine the appropriate balance between the number of locations, the number of years, and the number of replications for each test.

Baker (1969) analyzed tests of wheat cultivars in western Canada and found that the genotype × location and genotype × location × year interactions were significant, but the genotype × year interaction was not. He concluded that yield testing must be carried out at a number of locations, but that the number of replications at each location could be reduced without much loss of information. He also suggested that selection for regional adaptation would be desirable. In a later paper, Baker (1971) showed that much of the genotype × environment interaction was due to the effects of stem and leaf rust at some locations.

Other workers have used cluster analysis to group locations that give similar results, with the objective of reducing the number of test sites. Ghaderi et al. (1980) tested eight sites in Michigan and found that the removal of one resulted in a nonsignificant genotype × location interaction for the remaining seven. In Australia, Brennan et al. (1981) analyzed yield data for 6 yr at 15 to 27 locations. The cultivar × location, cultivar × year, and cultivar × location × year interactions were all significant, with the last usually being largest. To select for a widely adapted cultivar, they suggested a 4-yr testing program starting with a few locations that give different results and then gradually increasing the number of locations.

Campbell and Lafever (1980) analyzed data from 12 locations in the eastern USA for 7 yr. Cluster analysis tended to group locations that were in close proximity to each other. They also correlated the yields of cultivars in one location with the yields at every other location each year. The correlations ranged from −0.64 to 0.90, but in general the relative performance of entries at pairs of locations was not consistent from year to year. Because of the sizeable effects of years, the authors concluded that several years of testing is necessary and locations cannot be substituted for years.

Undoubtedly the balance between locations, years, and replications will depend on the size and variability of the geographic area being tested and the year-to-year variability in the weather.

7A–7 MIXTURES AND MULTILINES

The main effect of mixtures and multilines is to create genetic diversity within a population. This has two main purposes: (i) to produce

a more adaptable cultivar that will have increased yield, and (ii) to control disease by having genetic diversity for resistance within a cultivar.

Jensen (1952) pointed out the potential problems of genetic uniformity for disease resistance and suggested the use of multilines. Beginning in 1952 the wheat breeders at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico developed large numbers of isolines in 'Yaqui 50' (Borlaug, 1981). However, these became obsolete with the development of the semidwarf wheats. The first wheat multiline, 'Miramar 63', was developed in Colombia and proved to be highly successful in controlling stripe rust. More recently, three groups in India have done extensive work to produce multilines based on 'Kalyansona' (= 'Siete Cerros') (Gill et al., 1981; Singh et al., 1981; and Rao et al., 1981). Much of the current breeding program at CIMMYT involves the transfer of many types of disease resistance into a few high-yielding, recurrent parents (Rajaram et al., 1979). This material is then made available to wheat breeders in many countries, who can select out lines resistant to the diseases in their areas. One way of using the selected lines is in a multiline.

The basic idea in using a multiline to control a disease is that some components of the multiline will be resistant to each biotype of the pathogen. Thus, the development of each biotype will be slowed because a considerable number of its spores will land on resistant plants. The delay in the buildup of the epidemic is sufficient to protect the crop.

The evidence so far is somewhat limited but indicates that multilines are effective. The most extensive data comes from oat multilines in Iowa which have protected the crop against crown rust (*Puccinia coronata*) for a number of years (Browning et al., 1979). A considerable concern is the possible develoment of a "super race" that can attack all components of a multiline (Groth, 1976). Various models have been developed to predict the probability of a super race evolving. The accuracy of the prediction depends on the accuracy of the assumptions that are made. Only time will tell.

Breeders considering the use of multilines must keep several possible problems in mind. Developing multilines is slow, particularly if many backcrosses are used, and the recurrent parent may become out-of-date. Often several diseases are important and it is difficult to combine resistance in one multiline.

The use of simple cultivar mixtures as a possible way of increasing yield has been tested frequently in cereals. In some cases the mixtures had no advantage, in others they showed a small increase in yield over the average of the components, and sometimes over the highest component.

More recently, the use of cultivar mixtures has been recommended as a means of controlling several diseases in a crop, and both wheat and barley mixtures are being recommended in the United Kingdom (Wolfe et al., 1981). The mixtures usually contain three cultivars chosen to com-

plement one another so that part of the mixture is resistant to each biotype or disease. Data indicate that the mixtures provide effective disease control.

7A–8 CONCLUSION

Wheat breeders now have a considerable array of procedures available to them. Probably no two breeders use exactly the same procedure. Each selects a procedure that best fits his own situation and his own objectives.

7B Mutations and Mutation Breeding

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Mutations are the basic genetic variation on which natural evolution and artificial plant breeding depend. The plant breeder rearranges this genetic variation through the process of recombination and selection to improve the genotype. With the ability to induce mutations using artificial physical and chemical mutagenic agents, the breeder is no longer totally dependent upon nature for new germplasm resources.

The term *mutation breeding* originally applied only to the induction and selection of a mutant which was increased and used directly as a cultivar. This concept arose from the realization that the improvement of a single, simply inherited trait could be induced in a genotype while retaining the delicate balance of other traits (MacKey, 1956). Some examples of wheat cultivars from direct mutation breeding are listed in Table 7B–1. More recently, mutation breeding includes the combination of traits from two or more mutants in the same background to indirectly develop new cultivars. In *mutation cross-breeding*, mutant traits are recombined with those from other germplasm. Some examples are listed in Table 7B–2.

Direct mutation breeding can reduce the time for cultivar development and increase the benefits from a new cultivar (Sigurbjörnsson, 1972; Micke and Donini, 1982). Yamagata (1981) showed that in the diploid cereals, the time period for mutant cultivar development ranged from 4 to 7 yr (avg. 5.6), about half that normally required with cross-breeding. With indirect mutation breeding, cultivar development is extended by the time necessary to cross the mutant lines and recover recombinants. Mutation cross-breeding offers no time advantage, but some induced mutants, especially semidwarfs, already are preferred germplasm, demonstrating that selected mutant alleles may be uniquely valuable (Yamagata, 1981; Konzak et al., 1984a).

Mutation breeding methods should be viewed as complementary to others a breeder may use for cultivar development, depending upon the

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Table 7B–1. Wheat cultivars developed by direct mutation breeding (1960–82). Source: Based on information reported in Mutation Breeding Newsletters 1–23 (1972–1984), Sigurbjörnsson and Micke (1974), and Konzak et al. (1984a, 1984b).

Cultivar	Approval year	Initial material	Mutagen and treatment	Treatment year†	Country of origin	Improved trait(s)
Triticum aestivum						
Sirius	1968–1974	St. Noha/St.GZ Ho LiHe	2 cycles recurrent X-rays 15 krad/year	1951, 1952	Fed. Rep. Germany	Reduced height, lodging resistance
Els	1960	Single grain bulk Erli/Lichtifruh/*T. turgidum* ssp. *carthlicum*	3 cycles recurrent X-rays 1.3-2.5 krad	1953, 1954, 1955	Fed. Rep. Germany	Reduced height, lodging resistance
NP 836	1961	NP 799	X-rays 16 krad	1955	India	Awnedness, increased yield
Sinvalocho Gamma	1962	Sinvalocho	Gamma rays 20 krad	1956	Argentina	Stem and leaf rust resistance
Pusa Lerma	1971	Lerma Rojo	Gamma rays	1965	India	Amber grain color
Lewis	1964	Mo. W6185	Thermal neutrons	1954, 1956	USA-MO	Reduced height, lodging resistance
Stadler	1964	Mo. W6243	Thermal neutrons	1954, 1956	USA-MO	Reduced height, lodging resistance
Sharbati Sonora	1967	Sonora 64 A	Gamma 20 krad	1963	India	Amber grain color
Zenkouzi-komugi	1969	Igachikugo-Oregon	Gamma 30 krad	1959	Japan	Reduced height, earliness, lodging resistance
Novosibirskaja 67	1970	Novosibirskaja 7	Gamma 5 krad	?	USSR	Reduced height, lodging resistance
Nan Jing no. 3	1976	St. 1472/506	Gamma 25 krad	1968	PRC-Jiangsu	Reduced height, lodging resistance
Shirowase-komugi	1977	Shirogane-komugi	Gamma 25 krad	1966	Japan	Closed canopy phenotype

(continued on next page)

Table 7B–1. Continued

Cultivar	Approval year	Initial material	Mutagen and treatment	Treatment year†	Country of origin	Improved trait(s)
Hankkijas Taava	1978	Ruso	Gamma 20 krad	1966	Finland	Reduced height, lodging resistance
Jauhar-78	1979	Nayab	Fast neutrons	1972	Pakistan	Amber grain color
Shan Nong (Radio 63)	1980	F_4 line of You-bao/Ou-rou	Gamma 30 krad	?	PRC-Shandong	Earliness
Carolina	1981	Collafen	Gamma 10 krad	1972	Chile	Increased grain protein content
T. turgidum durum						
Castelporziano	1968	Cappelli	Thermal neutrons	1956	Italy	Reduced height, lodging resistance
Castelfusano (CP C48)	1968	Cappelli	Thermal neutrons	1956	Italy	Reduced height, lodging resistance
Castel del Monte	1969	Garigliano	Fast neutrons	?	Italy	Reduced height, lodging resistance
G-0367	1970	YG 3688	Thermal neutrons	1963	Greece	Reduced height, lodging resistance
Castelnuovo	1971	Garigliano	X-rays 4 krad	1958	Italy	Reduced height, lodging resistance
Durox‡	1981	Exp. line K6800707	EMS	1970	USA-WA	Reduced height, lodging resistance

†? = data unavailable.
‡Registered in France as Cargidurox; released in USA-Idaho, 1984, as Durox.

Table 7B–2. Some wheat cultivars developed using induced mutant gene resources. Source: Based on information reported in Mutation Breeding Newsletters 1–23 (1972–1984) and Konzak et al. (1984a, 1984b).

Cultivar	Mutant trait(s) transferred	Pedigree†	Country of origin
Triticum aestivum			
Odesskaja 75	Reduced height, lodging resistance	Karlik-1/Odesskaja-51	USSR
Odesskaja-Polukarlikovaja	Reduced height, lodging resistance	Karlik-1/Odesskaja-51	Hungary
Martonvasar 8 (Mv8, Claudia)	Reduced height, lodging resistance	Bezostaja I mutant/Ranka III mutant	Hungary
IAS 63	Stem rust resistance, shatter resistance	*Pel 19906-62/Pel 18102-62*	Brazil
Triticum turgidum			
Tito	Reduced height, lodging resistance	Castelporziano/Lakota	Italy
Augusto	Reduced height, lodging resistance	Castelporziano/Lakota/Castel del monte	Italy
Miradur	Reduced height, lodging resistance	Adur/Castelporziano	Austria
Attila	Reduced height, lodging resistance	Adur/Castelporziano	Austria
Grandur	Reduced height, lodging resistance	Adur/Castelporziano	Austria
Lozen 76	Reduced height, lodging resistance	788/2* Castelporziano	Bulgaria
Creso	Improved quality	Cp B144/5/Yt 54//N10 B14/3/2* Cp 63/4/3*Tc	Italy
Mida	Improved quality	Cp B144/5/Yt 54//N10 B14/3/2* Cp 63/4/3*Tc	Italy

†Mutant sources underlined.

problem, materials, and other circumstances (see also Brock, 1977). However, mutation breeding excels other methods in its potential for creating new genetic variation (or new combinations) from which major morphological or physiological modifications of a crop plant can be produced (MacKey, 1984).

7B–1 MUTATION BREEDING TECHNIQUES

Extensive information about mutagens, including specific safety practices to be employed and guidelines for mutagenizing seeds or pollen, are presented in the IAEA's *Manual on Mutation Breeding* (IAEA, 1977). Mutagen treatments applied to seeds are the most convenient. Direct and indirect mutation breeding requires greater attention to problem identification, planning, and the selection of initial materials than mutation cross-breeding. The latter requires greater attention to the selection of mutant alleles, associated mutant variation, epistatic gene interrelations, and to complementary parental materials. The potential and effectiveness of mutant materials in mutation cross-breeding may be influenced greatly by the care and criteria employed in selecting the initial material for mutagen treatments.

7B–1.1 Selection of Materials for Mutagen Treatment

In mutation breeding, the initial material usually is a single genotype or a population of closely related genotypes. Differences in genetic composition may occur both between and within the starting materials. The extent of diploidization/genetic redundancy may differ markedly between genotypes of polyploid wheats (MacKey, 1981a, 1981b; Konzak, 1981). Within a line or cultivar, genotype variability also is common, since in most breeding programs selection is discontinued before complete homozygosity is achieved. Because mutagens induce male sterility, natural crosses will occur between the genotypes present, even if the M_1 generation is properly isolated. For that reason, mutants induced in genetically variable materials may be genetically similar to only a part of the control population.

The ideal initial material for mutation breeding is an outcross-protected increase from the second selfed-generation of a single individual plant. However, the time necessary to develop such ideal starting material makes this approach largely impractical and necessary only for more theoretical investigations. The main requirement is uniformity for the obvious traits, especially those for which selection is likely to be practiced following the mutagen treatment. Suitable material often can be selected in the field from an elite stock increase or obtained by bagging spikes prior to pollination.

7B–1.2 Mutagens and Treatments

The selection of mutagens depends to some extent upon their availability, as well as on laboratory facilities, research objectives, and the nature of the material to be treated. Practical frequencies of viable mutations can be induced using ionizing radiations or chemical mutagens. Some aspects of these agents and typical application procedures are given below.

7B–1.2.1 Ionizing Radiations

The more penetrating hard x-rays (250 KvP), gamma rays (^{60}Co or ^{137}Cs), and thermal or fast neutron radiations have proved useful for mutagenizing seeds. Applications of the ionizing radiations should be made to resting seeds at 12.5 to 13% moisture as obtained by storage in a controlled atmosphere over a 60% glycerol solution (see Conger, 1972). Presoaking of seeds before radiation treatment usually results in lower mutation yields even if the effectiveness (i.e., mutations per unit dose) is greater. Doses of 10 to 20 krad ^{60}Co gamma radiation or ca. 1.5 krad fast neutrons are often applied to the resting polyploid wheat seeds following moisture adjustment. Immediate post-treatment rehydration, followed by drying of seeds at approximately 25°C for storage or planting seems desirable.

7B–1.2.2 Ultraviolet Radiation Treatments

The tissue penetration depth of nonionizing ultraviolet (UV) radiation from a mercury vapor gemicidal lamp (largely 2537 Å) is so low that its use is limited largely to single layers of cells, such as pollen. Because wheat pollen is so sensitive to dehydration, treatments must be made near the plants, with emasculated (or male sterile) spikes ready for pollination. Exposure to visible spectrum, shortwave (photoreactivating) light up to 480 nm (Auerbach, 1976), as in white fluorescent lamps, should be avoided to the extent possible. As with electromagnetic radiations, the dose is reduced in proportion to the distance squared. Ultraviolet radiation may find a greater role in applications to pollen or tissue culture systems currently being developed (A. Micke, FAO/IAEA, 1986 personal communication).

7B–1.2.3 Chemical Mutagens

The alkylating agents, particularly ethyl methanesulfonate (EMS) and diethyl sulfate (DES), have proved to be widely effective mutagens. These chemicals are readily available and present the least safety hazard among the more potent mutagenic agents. N-methyl nitrosourea (MNUA) and its ethyl analog (ENUA), as well as N-methyl and N-ethyl urethanes (MNU, ENU), are possibly the most effective and potent of all the chemical agents applicable to polyploid wheats (Konzak, 1981). However, high

carcinogenicity restricts their application to circumstances in which extreme safety precautions can be exercised. Azide (as NaN_3 or KN_3) for 1.5 to 3 h at 1 to 2×10^{-3} in pH 3 phosphate buffer is highly effective on diploid wheat, *T. monococcum* L., as in many other diploid species, but is less effective on tetraploid, *T. turgidum* L. var. *durum* (Desf.), and hexaploid, *T. aestivum* L., wheats, except as a complementary treatment (Konzak, unpublished). However, moderate mutation yields in hexaploid wheats have been obtained after azide treatment by others (Tavil, 1981) suggesting that effective azide treatments can be designed for polyploids.

All the chemical mutagens must infuse into the embryos through the seed-coat membrane (testa) before reactions with DNA of meristem initial cells are possible. The testa of cereal seeds is differentially permeable to positively charged chemicals (Wagner et al., 1968). Because of this, seeds often are presoaked for 1 to 16 h (4–6 h for azide, EMS, DES; 14–16 h for MNUA) at 20°C to facilitate rapid infusion of the neutral or noncharged chemical from and to initiate metabolic processes or DNA synthesis (de Kock, 1972; Kleinhofs et al., 1974, 1978). If the tissues are not hydrated, more of the reactions may be injurious to the physiological system (Konzak et al., 1965).

All buffers or other solution components, seed to be treated, sample containers, etc. should be prepared ahead of time at the desired temperatures. The pH 3.0, 0.1 *M* phosphate buffer is prepared by dissolving 12.0 g KH_2PO_4/liters of distilled water and adjusting to pH 3 with 1.0 *M* H_3PO_4 using a pH meter or indicator papers. However, the mutagen should be added just before the treatment is to be initiated, since all such active reagents are degraded by hydrolysis reactions with water.

7B–1.3 Mutagen Dose and Severity of Treatment vs. M_1 and M_2 Population Size

Moderate to low mutagen doses should be employed to reduce the frequency of plants carrying more than one mutation (Gaul, 1964; Konzak, 1981, 1984, unpublished). Severe mutagen doses should be avoided in polyploid wheats since excessive genome disruption may not only limit the total mutation yield, but also induce multiple mutants and large structural alterations, greatly reducing the frequency of single-locus mutants. Results from many experiments now strongly favor large M_2 populations, and less severe treatments for all applications. As the mutant frequency increases, the chances are greater that deleterious mutations will be induced in an individual carrying a useful mutation. In many instances, it has been found difficult or impractical to separate useful mutant genes from associated secondary genetic alterations by crossbreeding and/or selection (Sato and Gaul, 1967; S.E. Ullrich, Washington State Univ., 1985, personal communication; Konzak, unpublished).

Because low mutagen doses yield lower mutation frequencies, a larger M_2 population must be screened to obtain the desired number of mutants of a given type. The probability that a desired trait will be induced by a

mutagen treatment is low (Micke, 1984). In mutagenized materials, genetic variation is introduced de novo not entirely at random, with most segregation occurring in M_2. The population size required to obtain a desired number of useful mutants can be estimated theoretically (Yonezawa, 1975; Yonezawa and Yamagata, 1977). The rice (*Oryza sativa* L.) cultivar Reimei reportedly arose from an M_2 population of 50 000 plants (Yamagata, 1981). In contrast, 'Luther' barley (*Hordeum vulgare* L.) was one of just eight semidwarf mutants selected from about 5000 M_2 plants (Nilan and Muir, 1967; Konzak, unpublished).

Because the rate of mutability is a property specific to each gene and mutagen, much larger populations may need to be screened to isolate mutants of some loci compared to others. However, because certain phenotypes may result from mutations at any of several gene loci (e.g., reduced height), the frequency of a mutant type may be much higher than that for each specific locus.

The main limitation to direct mutation breeding is the compromise between the M_2 population size and the aforementioned low to moderate frequency of induced mutants in the population. The chimeric nature of the M_1 plant for mutated vs. nonmutated somatic tissues is a major cause of the high M_2 population requirement. Several schemes have been proposed to improve the relationship between population size and mutation yield by decreasing the nonmutant fraction. The aim is to exploit the fact that the main or apical spike of cereal plants carries the highest frequency of different mutants (Gaul, 1964). A high proportion of M_1 apical spikes can be obtained if the first emerging spikes are tagged (Sarvella et al., 1962; Frydenberg and Jacobsen, 1966). A simpler, but less exact, method is to sow the M_1 seeds at a high seeding rate and close row spacing to restrict tillering. Then bulk M_2 seed will yield a wider range and frequency of mutants than would be the case if the planting density permitted extensive tillering. Sampling one or a few grains per M_1 spike also may improve screening efficiency if space for the M_2 population is limited. However, more labor is required for the M_1 harvest and a large proportion of the M_1 material is wasted.

7B–1.4 Screening for Mutants

In direct mutation breeding, the frequency of a desired variant type in M_2 is orders of magnitude lower than in a cross-bred F_2, and similar mutant phenotypes may differ genetically (Micke, 1984). If the mutagen treatments have not been severe, most M_2 or M_3 individual plants will not differ notably from the control, and phenotype variants will be easy to identify by visual screening. Most mutants will be changed for one trait only or for a single complex of associated traits, such as in a speltoid. Enough M_2 material should be screened to allow for the recovery of several mutant individuals, perhaps carrying different alleles, because the mutants isolated may not all be of equal value or potential (see also Joshua and Bhatia, 1984). Consequently, efficient screening systems are

essential to success in direct mutation breeding, but cannot assure that a desired mutant type will be recovered. In seeking a new plant phenotype, Adams (1982) screened about 2.7 ha of bulk M_2 *Phaseolus* beans (< 500 000), but found only 12 progenies with the desired single stem, indeterminate but nonviny variant. However, the reduced height durum wheat mutant which became 'Castelporziano' was isolated from the progeny of only 950 M_1 plants from neutron-irradiated seeds (Donini et al., 1984). In contrast, Martens et al. (1983) grew about 7 000 000 M_2 plants of gamma-irradiated hexaploid oat, *Avena sativa* L., but obtained only one stem-rust resistant plant of poor type, from which the resistance could not be recovered. Perhaps in the latter case other mutagens should have been tried. Simons et al. (1983) induced mutations for increased or decreased tolerance to crown rust in comparatively small populations of recurrently EMS-treated hexaploid oats. However, the most rust-tolerant lines were low yielding. Cross-breeding to transfer the tolerance and/or screening of larger, one-time treated M_2 populations might have been more successful.

A skilled person can visually screen in one season several hectares of M_2 or M_3 wheat for characters such as height, maturity, awning, surface wax, and disease resistance. Mutant variations not readily detectable in a single individual or that are subject to significant environmental influences, such as yield or protein content, cannot be identified with comparable efficiency, but do occur and can be isolated (see Parodi and Nebreda, 1984). In some cases, visually distinct differences such as vigor may prove useful as indicators of yield improvement.

7B–2 TYPES OF MUTANTS INDUCED IN WHEAT

The relative proportion of mutant types induced in wheat shifts markedly with ploidy (MacKey, 1967). A large fraction of mutants induced in diploid wheat are chlorophyll-deficient forms. In contrast, the proportion of chlorophyll mutants in tetraploid and hexaploid wheats is low and largely restricted to one or a few types specific to the mutagenized genotype, apparently in direct relation to the extent of diploidization that has occurred. However, the proportion of viable mutations often is far greater in polyploid wheats than in diploids, and the total yields of mutations may be similarly high (MacKey, 1981a; Konzak, 1981). Different mutation spectra appear to be induced by different mutagens (e.g., by gamma radiation and MNUA), as recorded in M_2 populations from treatments to the cultivar Marfed, CI 11919 (de Kock, 1972).

7B–2.1 Induced Mutants of Specific Interest in Practical Breeding

Several classes of mutants commonly induced in wheat have potential not only for cross-breeding but also for direct release. Some of the classes will be described to illustrate the potential of induced mutants. Since similar phenotypes may be due to different mutants at different loci, the

classification of mutant phenotypes into groups may have little relation to their genotypes (Gustafsson and Lundqvist, 1981). Also, it is now abundantly clear from fine structure analyses of gene loci in maize and in barley that exact duplicate DNA base changes seldom occur among mutant alleles (Amano, 1972; Rosichan and Nilan, 1979; Kleinhofs et al., 1980). Consequently, desirable mutants should be considered unique and conserved in resource collections.

7B-2.1.1 Reduced Height (Rht)

Rht mutants are readily induced in virtually any genetic background (Gaul and Aastviet, 1966; Konzak, 1981) and those studied appear to represent new reduced height (*Rht*) alleles (Table 7B-3). Until recently, only four *Rht* genes had been extensively exploited in breeding (Table 7B-3). Of these, *Rht*1 and *Rht*2 trace to the old Japanese cultivars Shirodaruma and Akadaruma through the well known Norin 10, while *Rht*8 and *Rht*9 trace to an old Japanese land variety, 'Akakomugi', but came to the Western world after their introduction and exploitation by Strampelli in Italy (Dalrymple, 1978, 1980; Gale and Youssefian, 1985).

The associated short coleoptile length of the widely used *Rht*1 and *Rht*2 sources may severely affect seedling emergence and stand establishment of semidwarf wheat under low moisture conditions (Allan, 1980). The effects of *Rht8* and *Rht*9 on seedling emergence have not been evaluated sufficiently, but it may be significant that no dryland cultivars in the USA yet carry them, even though *Rht*8 and *Rht*9 have been available to breeders for many years. Consequently, in addition to the overall importance of diversifying the germplasm base of world cultivars, there is a need for new *Rht* gene sources. Many induced *Rht* mutants may have better emergence potential, since their coleoptile growth and gibberellic acid (GA) responses seem unaltered (Konzak, 1981).

Among the abundant new *Rht* mutants in bread wheat, the mutant Magnif 41 M1 (CI 17689) carries gene *Rht*13 which is different from *Rht*1 and *Rht*2, but with a similar semidominant behavior (Konzak, 1982, 1984; Konzak et al., 1984b). Its reduced height is not evident until heading, when internode elongation appears to be slowed. Even so, the peduncle is no more reduced relative to other internodes than in genotypes with *Rht*1 or *Rht*2, and the long spikes are identical to the original 'Magnif 41'. Mutant gene *Rht*20, in Burt M860, also is new, and while in the original mutant there appear to be secondary mutational changes, the new semidwarfing gene can be recovered and appears to be useful (Konzak, 1986).

Of special interest is the almost completely dominant gene *Rht*12 of the mutant Karcagi 522 M7K, a stabilized line (Konzak, 1984) from a mutant induced in Hungary using gamma radiation (Viglasi, 1968). Its associated spreading habit, thick, wide leaves, and late maturity require modification and this may take several breeding cycles. However, its slightly greater height reduction, strongly dominant character, strong stems,

Table 7B–3. Reduced height (semidwarfing) genes in wheat. Source: Adapted from Gale and Youssefian (1985); Konzak (1982, 1986), Konzak (unpublished); McIntosh (1973); Heiner and Elsayed (1974); and Pepe and Heiner (1975).

Rht gene	Chromosome location	Source	Origin†	Initial material	Associated GA3 Response‡	Dominance§	Use in breeding¶
*Rht*1	4A	Norin 10	S	Akadaruma?	I	P. dom.	Widest
*Rht*2	4Ds	Norin 10	S	Akadaruma?	I	P. dom.	Widest
*Rht*3	4A	Tom Thumb	S	?	I	Semidom.	Doubtful
*Rht*4	?	Burt M937 (CI15076)	M	Burt	S	Rec.	Doubtful
*Rht*5	?	Marfed M1 (CI13988)	M	Marfed	S	Semidom.	Doubtful
*Rht*6	?	Burt (CI12696)	S	(Brevor)	S	Rec.	Probably Wide#
*Rht*7	2A	Bersee Mut	M	Bersee	S	Rec.	Doubtful
*Rht*8	2D	Mara, Sava	S	Akakomugi	S	Rec.	Moderate
*Rht*9	7Bs	Mara††	S	Akakomugi	S	Rec.	Moderate
*Rht*10	4Ds	Ai-bian 1 (PI504466)	S	Abbondanza‡‡	I	Semidom.	Uncertain
*Rht*11	?	Karlik 1 (PI504549)	M	Bezostaja 1	S	Rec.	Some
*Rht*12	5A	Karcag 522M7K (PI503552)	M	Karcag 522	S	Str. dom.	Uncertain
*Rht*13	?	Magnif 41M1 (CI17689)	M	Magnif 41	S	P. dom.	Uncertain
*Rht*14	?	Castelporziano (PI347331)	M	Cappelli§§	S	Semidom.	Some
*Rht*15	?	Durox (PI478306)	M	K6800707§§	S	P. dom.	Promise
*Rht*16	?	Edmore M1 (PI499362)	M	Edmore§§	S	Semidom.	Promise
*Rht*17	?	Chris M1 (CI17241)	M	Chris	S	Rec.	Uncertain
*Rht*18	?	Icaro (PI503555)	M	Anhinga§§	S	Semidom.	Promise
*Rht*19	?	Vic M1 (PI503553)	M	Vic§§	S	Semidom.	Promise
*Rht*20	?	Burt M860 (PI503551)	M	Burt	S	P. dom.	Promise

†M = induced mutants, S = spontaneous, ? = unknown.

‡I = Gibberellin A3 insensitive, S = gibberellin A3 sensitive.

§P. dom. = partial dominant, Semidom. = semidominant, Rec. = recessive, Str. dom. = strong dominant. Partial dominant = partial recessive, Semidominant = greater dominance, Strong dominant = almost complete dominant.

§§Durums.

¶Doubtful = unless modified by additional genes; Some = recent use for several cultivars; Promise = good potential; Uncertain = good potential, but still under investigation—modification seems possible.

#Likely responsible for "triple dwarf" effect in breeding; has comparably smaller effect than Rht_1 or Rht_2.

‡‡Personal communication (Y. Dahue, PRC, 1984).

††By inference also in Italian *T. aestivum* 'Forlani' and 'Acciao', and *durum* derivatives 'Jucci', 'Montanari,' and 'Ringo,' based on geneology (Vallega, 1974).

and large, fertile spikes may have considerable agronomic value. *Rht*12 is located on chromosome 5A, a new linkage group for semidwarfing genes in wheat (Sutka and Kovács, 1987).

In the tetraploid durum wheats, genes *Rht*1 and *Rht*9 have been transferred from bread wheats (Vallega, 1974; Giorgi and Mosconi, 1982), but were accompanied by quality problems that only recently have been largely resolved for some *Rht*1 sources. Several promising new *Rht* gene mutants have been induced in high-quality durum cultivars (Table 7B–3). The now well known 'Cappelli' mutant, Castelporziano (Scarascia-Mugnozza, 1968; Scarascia-Mugnozza et al., 1972), has a relatively long coleoptile and its independent, semidominant *Rht*14 gene sometimes may have advantages over *Rht*1, since derivatives with either *Rht*1 or *Rht*14 appear to have similar yielding capacity (Giorgi, 1986).

Other new induced mutant semidwarfing sources in durums include the partially recessive gene *Rht*15 in 'Durox,' the partially dominant genes *Rht*16 and *Rht*19 in Edmore SD1 and Vic SD1, respectively, as well as a similar single gene *Rht*18 mutant from 'Anhinga' (recently released in Italy as 'Icaro'; L. Rossi, ENEA-FARE, Rome, 1985, personal communication). All four new mutants are GA_3 sensitive, and have long coleoptiles. Genes *Rht*15 and *Rht*18 are independent of *Rht*1 and of *Rht*14 (Giorgi et al., 1984; Konzak, unpublished; Rossi, ENEA-FARE, Rome, 1985 personal communication). The genetic relationships of Edmore SD1 and Vic SD1, to other *Rht* loci have not yet been established (Konzak, unpublished).

7B–2.1.2 Disease Resistance

Breeding for resistance to diseases and pests generally receives priority by wheat breeders throughout the world. As yet, there are few well-supported examples of mutagen-induced disease resistance in wheats and much more research under carefully controlled (contamination-free) conditions is needed. However, two reports stand out: the cultivar IAS 63, released in Brazil in 1974, was developed from an F_2 single plant selection of a cross between two M_2 mutants of 'IAS 20', one with improved stem rust resistance, the other with more shattering tolerance. IAS 63 yields more than IAS 20 and resists more rust races (Piexoto-Gomes and Carlos-Ignaczak, 1982). 'Sinvalocho Gama' (Table 7B–1) has improved stem and leaf rust resistance, induced by gamma radiation. Genetic analyses by Favret (1971, 1976) indicate some relation between changes in the reactions to the two rusts.

The potential for disease resistance mutations may be brighter than seems apparent from documented literature (Line et al., 1974; Konzak, 1981). Genes which suppress disease resistances are in fact surprisingly common. The presence of such genes offers opportunities, and possibly an explanation, for the artificial induction of certain types of disease resistance mutants. To date, several authors have shown that genes present in wheat suppress resistance genes (Law et al., 1978; Pink et al., 1983),

and particularly those introduced by alien species crosses or by synthesis of amphiploids (Quinones et al., 1972; Kerber and Green, 1980; Kerber, 1984). Moreover, resistance suppressor genes appear to be sufficiently common in hexaploid wheats to make impractical the search for null alleles by tester crosses (Kerber, 1984). The mutagen-induction of null alleles for the suppressors of resistance should be easily accomplished and some work is in progress (C. N. Law, Plant Breeding Institute, 1984, personal communication). As isogenic stocks, these types of mutants should prove useful for understanding the nature of host × pathogen interactions.

7B–2.1.3 Nuclear Male Sterility to Facilitate Cross-Breeding

Several male sterility mutants are now available. The induced recessive mutant *ms1c*, now termed 'Cornerstone' (Driscoll and Barlow, 1976; Driscoll, 1978), already is being exploited widely for developing male-sterile facilitated recurrent selection (MSFRS) populations in hexaploid wheat (Ramage, 1977; Driscoll, 1984).

A dominant genetic male sterility mutant induced in a *T. aestivum* stock carrying *Ae. squarrosa* (*T. tauschii*) cytoplasm also is in wide use as an aid in cross-breeding and for developing MSFRS populations (Konzak, 1984; Konzak et al., 1984a). This gene (*Ms3*), located near the centromere on the short arm of 5A was recently transferred to stocks with *T. aestivum* cytoplasm by exploiting the limited pollen fertility in the heterozygotes at controlled high temperature conditions (Maan and Williams, 1984; Maan, North Dakota State Univ., Fargo, 1986, personal communication). The dominant male sterility has the advantage that recessive, fertile F_1 progeny will produce only fully fertile progeny in subsequent generations. Also, if a simple gene restorer for *Ms3* can be found (which would seem feasible), the gene may prove useful for hybrid wheat development.

Recessive male sterility mutants are easily induced in both tetraploid and hexaploid wheats (Sasakuma et al., 1978; Konzak, 1984; K. Shantz, Western Plant Breeders, Phoenix, 1981, personal communication), and some are at loci other than *ms1* (K. Tsunewaki, Kyoto Univ., 1983, personal communication). Since *ms* mutants are easy to detect at flowering time, breeders may wish to induce *ms* mutants in their own locally adapted material.

7B–2.1.4 Physiological and Other Traits

Appropriate changes in crop phasic development may be important for advancing yield in cereals (Yoshida, 1972). Numerous mutants for physiological traits have been produced in several cereals (see Micke, 1979), but only a few such mutants have been used directly in breeding new wheat cultivars.

7B–2.1.4.1 Maturity. Earliness appears to be readily induced and

is easy to detect at heading (Solari and Favret, 1968). The frequency of earliness mutants appears to be lower than that for mutants which lengthen maturity (Konzak, 1981; Larik et al., 1984). Two early maturing wheat cultivars have been developed directly after gamma radiation treatment of seeds (Table 7B–1).

7B–2.1.4.2 Photoperiod Response. The potential of physiological mutants can be illustrated by the mutant HD2237 induced in India by Kar et al. (1978) from 'Kalyan Sona'. This mutant ripens 25 days earlier but yields more than Kalyan Sona. The vegetative phase is reduced from 102 to 70 days, while the generative phase is extended from 42 to 55 days. The grain weight of the mutant is 15% greater, tillering is more synchronous, and its height is 10-cm shorter than that of Kalyan Sona.

7B–2.1.4.3 Vernalization. *Vrn* locus mutations are readily induced. Such mutants have potential in breeding of new cultivars and for physiological and genetic analyses of the vernalization process. The *vrn* mutants of spring wheat do not noticeably affect winter hardiness (Konzak, unpublished), supporting the view that the vernalization response (so-called winter habit) and winter hardiness have a genetically distinct basis. Recessive *vrn* mutants in photoperiod-insensitive genotypes may offer the desired protection from cold injury in short-day environments (such as southern California and parts of Australia) by restraining flower initiation until cold weather can limit growth. In such cases, mutation breeding could effectively complement cross-breeding to accelerate cultivar development.

7B–2.1.4.4 Cuticle Wax. The character of the surface wax of plants may be an important trait for breeding (Hull et al., 1978). Johnson et al. (1983, 1984) found an 8 to 13% yield advantage for isolines carrying a chromosome 2D waxy gene under drought-stress cultural conditions in Western Australia. The waxy cuticle surface on wheat plants can be modified by induced mutation and the mutants are easily detected (Konzak, 1981, 1984, unpublished). Mutations either can increase or decrease the wax amounts, and often can change the polymer composition and structure of the waxes (Wettstein-Knowles, 1979; Wettstein-Knowles and Søgaard, 1980; see also Barbar and Netting, 1968; Kolattukudy, 1980).

7B–2.1.4.5 Awns. Awned mutants are easily induced in awnletted or awnless wheat genotypes. Awnless and partially awned mutants have been induced in durums (Shkvarnikov and Kulik, 1975) but have been found only once in an awned hexaploid (Konzak, unpublished). NP836, released in India in 1961, was developed by converting an awnless to an awned genotype (Sigurbjörnsson, 1972). Konzak (1981) found awned mutants useful in the development of more truly isogenic lines (also see Zeven et al., 1983; Zeven, 1984) for research. Since awns may contribute favorably to yield in some environments, there is good potential for exploiting awned mutants using mutation breeding techniques.

7B–2.1.4.6 Protein. Research to improve protein in wheat has been limited because until now comparatively efficient screening and analysis methods for detecting protein mutants have not been available. However, 'Carolina', developed in Chile via direct mutation breeding, has the capacity to produce higher protein content grain than the original 'Collafen' without sacrificing yield (Parodi and Nebreda, 1982a, 1982b). Results from other studies indicate that mutant TW-1 produced in Pakistan (Bhagwat et al., 1979), a series of mutants produced at FAO/IAEA, Vienna (Hermelin, 1984), and others isolated in Chile (Parodi and Nebreda, 1984) may be among the more promising new mutant materials developed for increasing grain protein content. TW-1 has been proved to genetically transmit its high protein trait to higher yielding progeny (Bhagwat et al., 1979; Brunori et al., 1980, 1984).

Wheat mutants with increased lysine content have been reported from the USSR (by Lukyanenko: F. Zhogin, Krasnodar, USSR, 1983, personal communication), the USA (Konzak, 1981), and Argentina (Favret et al., 1984). The Argentine mutant has a shrunken endosperm much like Riso 1508 in barley (Tallberg, 1982), whereas wheat mutant MJD72175 (Konzak, 1981) has a normal endosperm. A consistent feature of the wheat mutants is their weaker dough mixing properties.

7B–2.1.4.7 Plant Form. Stable variants affecting plant form and apical dominance are frequent in both hexaploid and tetraploid wheats (de Kock, 1972; Konzak, 1981; Konzak, unpublished). The cultivar Shirowase-Komugi was developed directly from 'Shirogane-Komugi' in Japan (Table 7B–1) and has a more desirable closed plant stature (Toda et al., 1972).

7B–2.1.4.8 Leaf Size, Shape, and Attitude. Vital mutants with changed leaf length, width, thickness, and erectness or without ligules can be induced with mutagens (de Kock, 1972; Konzak, 1981). Some of the mutants may be useful in breeding, while others may be of interest for physiology studies.

7B–2.1.4.9 Spike Form. Stable, *compactum*-like mutants appear to be inducible in both hexaploid and tetraploid wheats, though these occur more rarely than do lax spike forms from the compact genotypes (Sharma-Rao and Sears, 1964; Konzak, 1981). The wide range of speltoid and near-speltoid mutants induced in wheat offers scope for studies of this trait, and when induced in modern genotypes may provide useful new germplasm for shattering resistance.

7B–2.1.4.10 Glume Length, Glume Shape, Grain Size. Changes in glume morphology and in size and shape of grains are common in M_2 mutagenized cultures (de Kock, 1972; Konzak, 1981). Rounded glume variants include, but are not limited to, several *sphaerococcum*-like forms, in which a complex of traits may be affected.

7B–2.1.4.11 Grain Color. When the grain seed-coat color is con-

trolled by a single dominant R gene pair, as in 'Novosibirskaya 7', rather than by two or three R genes, mutation breeding may be an efficient means to convert a red to a white grain genotype, as was achieved in Novosibirskaya 67 (Lbova and Cherniy, 1979) and several other wheats (Table 7B–1).

7B–3 CONCLUSIONS

With the development of mutation breeding methods the plant breeder need not be limited to the genetic resource base immediately available or present in unadapted germplasm stocks. Experience indicates that it should be relatively easy and straightforward to induce certain types of mutant, such as semidwarfs, in locally adapted lines or cultivars. The range and frequency of mutants induced may differ not only with the mutagen and treatment (especially pregermination period), but also with the genotype of the material treated. Different loci may produce similar mutant phenotypes, and it is common to discover previously unknown and unexpected genetic loci for a given character via induced mutation studies. Using techniques favoring the induction of single mutants, one may subject induced mutants to field tests by the M_3 or M_4 generation. Certain mutants are directly usable as cultivars. However, some mutants are proving even more valuable as germplasm for cross-breeding to produce higher-performing cultivars. A few mutant types now known may sufficiently modify plant growth patterns and plant structures to have a major impact on the character of future cultivars.

Induced mutants also provide the breeder with ready material for genetic investigations aimed at germplasm development. Mutants may be more nearly isogenic to their original parent stock than isogenics produced by backcrossing and thus may offer plant physiologists and biochemical geneticists more efficient probes for investigating plant processes.

The most successful uses of mutation breeding complement conventional methods but depend on the creative knowledge and imagination of the breeder. Breeders should not be discouraged if a desired objective is not reached using direct mutation breeding since few of the many hundreds of conventional crosses ever result in new cultivars. One or more of the three approaches to mutation breeding may prove effective, but the method and materials, including parents or initial materials, must be appropriate for the objective. Success in direct mutation breeding requires not only careful selection of the initial materials but also appropriate management thereafter. With careful planning and following of objectives, short-term goals may be achieved with particular efficiency via mutation breeding methods, while the potential for creating new gene resources offers a measure of uniqueness in approaches toward the longer-term goals of a modern plant breeding program.

7C Hybrid Wheat

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Most of the developmental research on hybrid wheat is being done by commercial seed and chemical companies. Several recently published reviews on hybrid wheat describe this research and provide a comprehensive overview of the current status and prospects for hybrid wheats (Wilson and Driscoll, 1983; Virmani and Edwards, 1983; Wilson, 1984; McRae, 1985). This section will describe some of the genetic variation used for hybrid wheat development and will discuss procedures for breeding parents for hybrids.

7C–1 CYTOPLASMIC MALE STERILITY AND MALE FERTILITY RESTORATION

Cytoplasmic male sterility in wheat is a derived trait, first described by Kihara (1951). He transferred the genomic complement of one species into the cytoplasm of a second species by backcrossing, using the nuclear donor parent as pollen parent in the initial cross and in successive backcrosses (substitution backcrossing). Kihara found that plants in which the genomes of *T. aestivum* had been substituted into the cytoplasm of *T. dichasians* Zhuk. were male sterile and had pistilloidy. Subsequently, Fukasawa (1953) backcrossed the *T. durum* L. genomes into the cytoplasm of *T. ovatum* L. The resulting plants were male sterile and had delayed heading.

These findings and their potential use in hybrid wheat breeding prompted Wilson and Ross (1962) to seek another cytoplasm that would cause male sterility without causing deleterious effects. They reported that the interaction of *T. timopheevii* Zhuk. cytoplasm and the *T. aestivum* nucleus resulted in a complete and constant male sterility. Furthermore, the *T. timopheevii* cytoplasm had no apparent adverse effects on plant growth and development.

Since 1962, wheat geneticists in Japan, the USA, and Bulgaria have found some 15 to 20 cytoplasms that differ from one another and from

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T. aestivum cytoplasm (Maan, 1975; Tsunewaki et al., 1980; Panayotov et al., 1975; Sage, 1976). Several cytoplasms reduce vegetative growth or delay maturity, restricting their use for hybrid breeding.

The nuclear-cytoplasmic interactions from which cytoplasmic male sterility is derived can be described as primary or secondary. When substitution of the entire genome complement of one species into the cytoplasm of a second species results in male sterility, the sterility can be termed *primary*, (e.g., the male sterility obtained when the *T. aestivum* genomes are substituted into the cytoplasm of *T. speltoides* Tausch).

Secondary male steriles are those obtained from a nuclear-cytoplasmic interaction between alloplasmic *T. aestivum* and a gene or chromosome introduced into the *T. aestivum* genome from a third species. For example, Mukai and Tsunewaki (1979) reported male sterility in wheat plants that had *T. kotschyi* Boiss. cytoplasm and chromosome 1B of *T. aestivum* var. *spelta* (*duhamelianum*). Based on this interaction, they proposed a system for breeding hybrid wheats in which normal *T. aestivum* would serve as the male parent. Wheat plants that have the 1B/1R rye (*Secale cereale* L.) substitution exhibit a similar male-sterile interaction, again allowing the use of normal *T. aestivum* as the male parent (Panayotov and Gotzov, 1981).

Franckowiak et al. (1976) have suggested a pollination control system based on alloplasmic *T. aestivum* with *T. tauschii* Coss. cytoplasm. Rather than introducing a nuclear gene from a third species, however, they proposed to use a mutagen to induce a nuclear gene mutation for male sterility that is specific for *T. tauschii* cytoplasm. Normal, euplasmic *T. aestivum* would serve as the male parent in hybrid production.

Another approach for producing hybrid seed uses a nuclear gene for male sterility and an alien chromosome to obtain a pollination control system (Driscoll, 1972; Wilson and Driscoll, 1983).

Breeding to achieve complete fertility restoration in F_1 hybrids has set the pace of hybrid wheat breeding for many years. The initial *Rf* genes were derived from *T. timopheevii* and from a *T. aestivum* line with *T. timopheevii* parentage (Wilson, 1962; Schmidt et al., 1962; Livers, 1964). Other *Rf* genes for the *T. timopheevii* system, mostly for partial restoration, were found in a few bread wheats or were introduced from related species.

The first attempts to introduce *Rf* genes into agronomically adapted wheats by backcrossing almost invariably failed to produce R-lines that would confer complete male fertility to their F_1 hybrids with male steriles having *T. timopheevii* cytoplasm. Most *T. timopheevii*-derived R-lines have *Rf* genes on 1A, 6B, 7D, or on some combination of these chromosomes. An *Rf* gene or genes found in 'Primépi' and some European wheats and located on chromosome 1B also have been used extensively in R-line breeding. Although the *Rf* genes on chromosomes 1A, 6B, and 1B appear to be the major genes used in most hybrid programs, *Rf* genes or their modifiers have been located on 17 of 21 chromosomes (Sage,

1976). R-line breeding programs, therefore, must be designed to select for complementary *Rf* gene combinations, to accumulate favorable modifier genes, and to eliminate inhibitory genes. This selection process is complicated by the fact that the fertility of an R-line that has *T. timopheevii* cytoplasm provides only a partial indication of restoration in F_1 hybrids; that is, the *Rf* genes are more effective when homozygous than when heterozygous.

Male fertility restoration is the restitution of normal anther and pollen development to wheat plants that have the male-sterility inducing cytoplasm. In populations segregating for *Rf* genes, plants often range from completely male sterile to completely male fertile. The most useful criterion for fertility restoration from a breeding viewpoint is anther extrusion (Ghiasi et al., 1982). Thousands of plants or head-rows can be screened visually for complete anther extrusion to the tip of the head. Anther extrusion data from replicated yield trials provide the best estimates of the self-fertility of an R-line. Visual examination of anther appearance can be used to supplement anther extrusion as a criterion for fertility restoration, particularly in testcrosses.

The short duration of anthesis within a wheat nursery is the major limit to assessing anther extrusion. Consequently, visual evaluations of seed set, estimated at or near maturity, often are used as the primary selection criterion in early generation R-line populations and also in testcrosses.

In breeding R-lines, a pedigree-testcross system normally is used, with crosses made so that segregating populations have male-sterile cytoplasm. The crosses may be A-line/R-line, R-line/B-line, or R-line/R-line. In the F_2 and subsequent generations, selection is practiced for self-fertility. Beginning in any generation, but usually in the F_4 or later, the R-line is testcrossed with a male sterile, and the resulting F_1 progeny is evaluated to determine the fertility restoration potential of the R-line.

Results from several hybrids grown in an International Wheat Restorer Germplasm Screening Nursery show that there is an unusually high degree of instability and environmental sensitivity associated with fertility restoration (Jošt and Lucken, 1983). These environmental and genotypic effects have contributed to the difficulty in developing R-lines for some wheat-growing regions. The apparent differences between genotypes in compatibilities with *Rf* genes may be due to genes that modify the expression of the *Rf* genes. There is substantial evidence for such genes, although they are difficult to study and to characterize. The evidence for this includes, first, the fact that the male-sterile parent can contribute nearly as much to variation in seed set of F_1 hybrids as the R-line parent and, second, the results of monosomic analyses (Jošt and Lucken, 1983; Sage, 1976).

In a monosomic analysis of R113, Maan et al. (1984) found only two major *Rf* genes (on chromosomes 1A and 6B) but detected modifier genes, or *Rf* genes of low penetrance or expressivity, on eight other chromo-

somes. They concluded that the high fertility restoration potential of this line resulted from the cumulative effects of the *Rf* genes plus modifiers. Their results suggest that the incorporation of favorable modifier genes for fertility restoration into the female parent merits examination.

The best R-lines are now comparable to conventional cultivars for most agronomic traits. These R-lines represent a unique germplasm pool, comparable with or parallel to that of conventional breeding programs, yet having introgressed cytoplasm and nuclear genes which broaden the germplasm base of cutivated wheats.

7C–2 CHEMICAL HYBRIDIZING AGENTS

A more recent and alternative system for producing hybrid wheat is through the use of chemicals that induce male sterility, thus circumventing the use of genetic pollination control systems. To produce hybrid seed, the female parent (a conventional wheat cultivar or line) is treated with the chemical at some stage before anthesis, and the resulting male-sterile plants are pollinated by wind-borne pollen from alternating, untreated male parent drill-strips.

Several chemical companies have programs to synthesize, identify, and evaluate the performance of potential chemical hybridizing agents. Much of the knowledge about these chemicals, including chemical structure, potential modes of action, and optimal treatment procedures, is proprietary and has not been published. These chemicals are now being described as *chemical hybridizing agents* (CHAs) or pollen suppressants, rather than as male gametocides.

The discussion that follows, describing the performance of CHAs and the requirements for CHAs, is general and is based on research described in several papers, including the following: Rowell and Miller, 1971, 1974; Jan et al., 1974; Miller and Lucken, 1977; Johnson and Brown, 1978; Johnson, 1984; McRae, 1985.

The requirements for an effective CHA are exacting. The chemical must induce complete or near-complete male sterility without reducing female fertility. It should be systemic, or sufficiently persistent to sterilize both early and late tillers. The sterilizing action of the CHA should extend for several days before and after the optimal treatment time to give the seed producer adequate time to treat all his seed production acreage. Furthermore, other effects of the CHA on plant development and plant growth should be minimal. Plants treated with CHAs have shown slight to severe phytotoxic effects. Generally, the phytotoxic effects are readily recognized, particularly at high dosages. Substantial progress has been made in synthesizing chemicals in which the major deficiencies of earlier CHAs have been minimized or overcome.

The potential use and versatility of CHAs also will depend on genotype by chemical interaction, on environment by chemical interaction, and on genotype $\times$ chemical $\times$ environment interaction. Tailoring ap-

plication rates and timing to each female parent likely will be necessary to assure maximum seed production. Large interactions, however, could mean variable and less predictable performance and could cause problems in CHA hybrid seed production.

The results from most investigations of CHAs indicate that there is genotypic variation for response to a CHA. The nature of this variation is not known; furthermore, differences among wheat cultivars and lines for cross-pollination potential and for developmental stages at the time of CHA application make variable responses to a CHA difficult to measure.

Prospective CHAs must be tested in experiments involving properly designed crossing blocks to assess male sterility and female fertility. Male sterility normally is determined by bagging wheat heads of treated plants with a glassine bag prior to anthesis and by weighing or by counting the seed at maturity. Female sterility is determined by measuring seed set from cross-pollination on wheat plants treated with a CHA. The values obtained for seed set, however, can be increased (if the CHA does not cause complete male sterility) or decreased (if seed set by cross-pollination is $< 100\%$, the typical situation within wheat crossing blocks). To obtain accurate measurements of female sterility, the level of male sterility of treated plot and the cross-pollination potential within the experiment also must be determined. A measure of the latter can be obtained from seed set on untreated cytoplasmic male steriles. Seed set data can also be obtained by hand-pollinating heads on treated plants.

The availability of CHAs raises questions about the relative merits of genetic and chemical production of hybrid seed. The two types of hybrid seed production technology share many common goals and problems. However, each has unique problems as well, and requires substantial investment of time and money to refine and to implement.

The CHAs have two principal advantages. First, breeding of parental lines is simplified because breeding operations to manipulate cytoplasm and restorer genes are eliminated. A CHA can be used to produce hybrids between almost any wheat cultivars and lines in experimental quantities. From a commercial standpoint, however, the statement must be qualified. Most cultivars or lines from conventional breeding programs cannot be used directly as hybrid parents because they lack the floral and head characteristics needed for high, economical cross-pollination in hybrid seed production fields. Male parents must be chosen on the basis of high anther extrusion and pollen production and female parents on the basis of their capacity to give high seed sets through cross-pollination.

Second, CHAs eliminate most of the problems associated with the seed increase of parents. There is no need for separate crossing fields to increase male steriles, thereby eliminating the most costly and difficult seed operation required with genetic systems. The lead time for increase of the female parent is decreased by 2 or more yr.

The advantage of genetic pollination control systems is simply that

the female parent in hybrid seed production fields is already male sterile. With a CHA, the seed producer must apply the chemical to the entire acreage of the female parent within a prescribed time (the length of which can vary among CHAs). In some seasons in some environments, wind, rain, and wet soil conditions could make this a formidable undertaking. Conversely, should drought or other growth stresses make low, unprofitable hybrid seed production probable, the seed producer using a CHA has the option of abandoning hybrid seed production and harvesting a normal wheat crop instead.

7C–3 BREEDING OF PARENTS AND EVALUATION OF HYBRIDS

Relatively little research has been reported on the management of germplasm in a hybrid wheat breeding program. Three distinct breeding operations must be coordinated: R-line or pollinator development, A-line or female parent development, and hybrid production and testing. Female parents, and probably male parents as well, should possess the same performance attributes as conventional cultivars to assure high, reliable yields of hybrid seed in hybrid production fields; that is, they should be superior lines. Consequently, the breeding, selection, and testing of hybrid parents will parallel that for conventional cultivars.

The breeding of hybrid parents requires six additional testing and evaluation steps for a genetically based system, four of which apply to a CHA-based system. These are as follows: (i) evaluating the male fertility restoration of R-lines in testcrosses; (ii) backcrossing female lines into *T. timopheevii* cytoplasm and increasing seed of male steriles; (iii) determining seed-setting capacity of female lines; (iv) determining pollinating capacity of male lines; (v) determining combining ability of female lines; and (vi) determining combining ability of male lines. Although each of these steps is a separate testing operation, the limitations they impose on the numbers of genotypes evaluated during parental development can be reduced by careful planning and by proficiency in using CHAs or in evaluating fertility restoration.

The dominant variable in hybrid seed production economics is seed set on the male-sterile parent through cross-pollination. A primary goal for hybrid wheat breeders, therefore, is to improve and to stabilize the cross-pollination capacity of this normally self-pollinated crop.

The quantity of pollen released over a wheat field and the access a wheat floret provides to airborne pollen are functions of several morphological and physiological characteristics of the wheat head and flower, which can vary among genotypes. Genotypes differ in anther length, anther width, anther size, floret opening, anther extrusion or open flowering, filament length, pollen grains per anther, pollen grains per anther shed outside the floret, flowering pattern and duration, lodicule size, and head

compactness (for specific references, see de Vries, 1971, and Atashi-Rang and Lucken, 1978).

It is not feasible to measure these characteristics in a breeding program where thousands of potential parental lines must be evaluated. Fortunately, hybrid breeders have identified rapid, simple screening criteria and procedures for improving the cross-pollination capacity of both male and female parents.

For the pollinator parent, the most useful selection criterion is anther extrusion, discussed above. This trait varies substantially among wheat cultivars and lines, and its response to selection compares favorably with that for agronomic traits (Ghiasi et al., 1982).

A direct measure of pollinating capacity is obtained only in crossing blocks from seed sets on females interplanted in strips with the pollinator. The isolating distances from other wheat required for crossing blocks typically limit the number of pollinators that can be evaluated to fewer than 20 or 30. The seed sets also reflect traits that increase pollinating capacity beyond that obtained from selection for anther extrusion, e.g., pollen buoyancy, viability, and durability, as well as the floral traits mentioned above.

The best selection criterion for seed yields on male-sterile plants is seed set itself. Seed set on male-sterile plants can be determined from harvested yield, from sampled heads, and, most significantly from a screening perspective, from visual estimates taken at or near maturity (Johnson, 1984).

Breeding programs that have access to CHAs can screen early generation populations for seed set. Head-row nurseries of several thousand genotypes, planted as crossing blocks, with alternating pollinators, can be treated with a CHA and screened visually for seed set. The progression of (selected) genotypes with advancing generations, grown in larger plots at more sites, also can be routinely assessed for seed set using a CHA. Such selection should improve cross-pollination capacity of females, increase the gene frequency for floral traits that contribute to high seed sets, and possibly identify genetic variation in wheat or its relatives which will minimize environmental effects on seed setting capacity.

The number of inbred lines, male and female, that a hybrid program can develop far exceeds the number that can be evaluated for their combining ability. The total number of entries, inbreds plus hybrids, that any program can test in yield trials is limited by project resources. To identify superior parents, therefore, a decision must be made about the relative merits of yield-testing parents per se, as compared to testing their performance in hybrid combinations. (Wilson, 1984, discusses this problem.) Numerically, the question is one of the relative efficiency of yield testing f + m parents (number of females + males) as compared to that of testing f × m hybrids, or some combination thereof.

Most programs do extensive inbred yield testing, particularly for the female parent, before testing an inbred in hybrid combinations. The as-

sumption here is that high-yielding inbreds are more likely to have high general combining ability. Furthermore, many traits essential to hybrid perfomance (disease resistance, maturity, plant height, straw strength, test weight, milling and baking quality, for example) can be effectively screened in inbreds.

Testers to evaluate the combining ability of inbred lines are chosen on the basis of their combining ability and their seed production potential. They likely will include inbreds that have commercial potential as male or female parents and will be changed as lines superior to them are identified. The progression of combining ability evaluations from initial screening to final hybrid testing, and the choice and number of testers will depend on how useful testers prove in identifying superior inbreds. The use of CHAs also could shift the balance between inbred and hybrid testing toward actual hybrid testing, resulting in rapid, recurrent cycling of genotypes and greater genetic gains.

Genetic diversity as indicated by pedigrees, geographical origin, and morphological and adaptive diversity is regarded as essential for the expression of hybrid vigor. It must be considered in the choice of parents and selection of germplasm for use in parental breeding. Extensive hybrid testing for grain yield should define further sources of genetic diversity useful for developing hybrid parents.

Increments of yield contributed to hybrid performance by the female parent and by the male parent as a result of systematic screening for combining ability should extend hybrid advantage beyond that of current hybrids. How effective direct F_1 progeny testing is for determining combining ability and genetic diversity should become known as breeding programs achieve the ability to routinely screen hundreds of hybrids in standard yield trials.

The selection of parental germplasm also is influenced by opportunities to use parent complementation or multiplicative gene effects to hybrid advantage. Yield components, milling and baking characteristics, adaptability and stability, maturity, plant height and straw strength, and disease resistance are amenable to such complementation. Wilson et al. (1980), for instance, have described the use of females which carry both of the recessive semidwarfing genes Rht_1 and Rht_2 to deal with the problem of excess height and lodging in hybrids. These full-dwarf females are too short for most commercial production, but hybrids between them and males which have one semidwarfing gene produce hybrids of a height that is optimal for maximum yields in some areas.

The first efforts of hybrid programs to evaluate hybrid performance usually were made by testing hand-produced hybrids between adapted cultivars and lines. (Wilson and Driscoll [1983] and Virmani and Edwards [1983] have reviewed some of the work on hybrid vigor and combining ability in wheat.) A second group of hybrids, tested during the 1970s, were early products of programs using the nucleo-cytoplasmic system. Partial fertility restoration or agronomic deficiencies in the par-

ents probably detracted from the performance of these hybrids (Johnson, 1977; Allan, 1973; Hayward, 1975; Hughes and Bodden, 1978). Finally, the current status of hybrid wheat development is reflected by the performance and numbers of hybrids being tested in the hard red winter wheat region of the USA (Walter, 1983; Smith et al., 1984). In the 1983 Kansas State Wheat Performance trials, for example, 20 of 55 entries were hybrids. Guenzi (Kansas State University, personal communication, 1984) summarized and compared yield data from several hybrids and cultivars grown at 52 locations in Colorado, Kansas, and Oklahoma in the hard red winter wheat region during 1982–83. Mean yield of the hybrids was 4322 kg ha $^{-1}$, compared to 4013 kg ha^{-1} for the cultivars, an 8% advantage for the hybrids. In Oklahoma, the best hybrid outyielded the best check by 17%.

7C–4 SUMMARY

Currently, hybrid wheats are being routinely produced, tested, and evaluated by several hybrid wheat programs. Technical capabilities for controlling pollination to produce hybrid seed continue to expand, increasing the numbers of experimental hybrids tested and the efficiency with which hybrids are evaluated. Although genetic and chemical pollination control systems are competitive in commercial application, the availability of both extends the hybrid wheat breeder's ability to find, manipulate, and use genetic variability to develop superior hybrid parents.

Genetic variation to improve the cross-pollination capacity of hybrid wheat parents has been identified and is being routinely incorporated into hybrid wheat parents. Procedures by which segregating populations of male lines can be screened for their potential pollinating capacity and populations of female lines for their seed-setting capacity should enable hybrid breeders to enlarge further the cross-pollination potential of hybrid parents, reducing the costs of producing hybrid seed.

As parental germplasm is improved and proficiency in producing seed of experimental hybrids increases, the contributions of hybrid breeding methodology, genetic diversity, and superior combining ability to hybrid yield advantage in wheat will be explored more definitively.

7D Interspecific and Intergeneric Hybridization in Wheat

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The major objectives of wide hybridization in the Triticeae have been to increase the extent to which species of *Triticum* L. and related genera can be crossed with one another, to establish phylogenetic relationships among the species and genera, and to produce synthetic amphiploids for transferring desirable alien genes to the cultivated wheat species.

The purposes of this section are to state the need for collection, maintenance, and evaluation of the available genetic diversity among the species of *Triticum* and related genera, to discuss obstacles to the use of alien germplasm, and to summarize literature on wide hybridization involving species of *Triticum*.

The classification of the *Triticum* and *Aegilops* L. spp. given in section 5 A-1 above, will be followed, and for the *Agropyron* Gaertn. and related species the classification described by Dewey (1983) will be used. However, to avoid confusion, in referring to the literature the designations used by the authors will be given and in some cases followed by the new designations or common synonyms.

7D-1 COLLECTION, MAINTENANCE, AND EVALUATION OF ALIEN GERMPLASM

The cultivation of wheat in a variety of climates in many countries and the wide geographical distribution of species of *Triticum* and related genera indicate that an abundance of genetic variability is available for research on broadening the genetic base of wheat. The phylogenetic relationships among the species of *Triticum* and related genera, artificial synthesis of hexaploid wheat (McFadden and Sears, 1946), and production of a large number of interspecific and intergeneric hybrids (and am-

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phiploids) in Triticeae (Kimber, 1979) indicate that certain desirable alien genes can be transferred to wheat chromosomes.

For the last several decades, progressively fewer high yielding crop cultivars have been widely adapted and grown over large contiguous tracts of land in many countries. New improved cultivars have replaced native land races of wheat in many countries. To meet growing human need, forest and grasslands are being reclaimed to grow more food and fiber crops. Consequently, wild species of wheat and related genera are being lost in their natural habitats, where grasslands have been reclaimed or domestic animal grazing extended to previously conserved areas. As a result, long established ecosystems have been imbalanced, genetic vulnerability of the wheat crop to pests and environmental hazards has been increased, and the genetic base of the wheat crop has been narrowed (Anonymous, 1972, 1978). Therefore, collection, maintenance, and evaluation of wild species of *Triticum* and related genera have been of continuing concern to wheat scientists of many countries (Vavilov, 1926; Kihara et al., 1965; Yamashita, 1968; Zohary et al., 1969; Brezhnev, 1977; Moseman et al., 1978; Hondelmann, 1978; Feldman and Sears, 1981; Limin and Fowler, 1985; McGuire and Dvorak, 1981; Sharma et al., 1981).

It is essential that the available collections of wild species of *Triticum* and related genera be preserved and periodically evaluated for desirable genetic traits prior to their use in wide hybridization programs. Collections should be tested for reaction to the prevalent physiologic races of pests that attack a wheat crop in a given area. Accessions with combined resistance to several pests should be the most desirable ones to use as donors of useful genes to wheat. Pest resistance of alien species have been evaluated at several research institutions in the USA (Moseman et al., 1978; Hatchett et al., 1981; Harvey et al., 1980; Joppa et al., 1980; Gill et al., 1983), Canada (Kerber and Dyck, 1978), Australia (Halloran, 1974), and other countries (Kihara et al., 1965; Pasquini, 1980; Vallega, 1978).

The procedures involved in the evaluation and testing of a large number of accessions for reaction to several strains of several pests is a formidable task. Therefore, utilization of alien germplasm for wheat improvement requires cooperation among wheat breeders and other scientists such as geneticists, pathologists, and entomologists. Nevertheless, by using international nurseries, substantial progress has been made in selecting elite germplasm of *T. aestivum* for resistance to cereal rusts (Kilpatrick and Moseman, 1978).

Once alien sources of useful genetic traits are identified, attempts can be made to obtain hybrids with wheat, and methods can be developed to select segregants with desirable traits in the hybrid progenies.

7D–2 CROSSABILITY OF SPECIES

Many species of *Triticum* and related genera are cross-compatible, and hybrids between species belonging to the same as well as different

genera can be produced (Knobloch, 1968). In general, most interspecific and intergeneric hybrids involving species of *Triticum* are highly male sterile, but they produce backcross progeny from pollination with parental or other related species. Polyploid species are easier to cross as females than as males in crosses between the diploid and polyploid species. Also, there is substantial intra- and interspecific variability in cross-compatibilities among the species of *Triticum* and related genera.

Snape et al. (1979), Falk and Kasha (1981), and Tanner and Falk (1981) reported a high correlation between the crossability of specific wheat cultivars with *Secale cereale* L. and with *Hordeum bulbosum* L. Thomas et al. (1981) reported that wheat cultivars giving high seed set in crosses with rye also had high seed set with pollen of several species of *Triticum*, *Agropyron* Gaertn., *Elytrigia* Desaux, *Secale* L., and *Elymus* L.

The crossability of wheat and rye was reported to be controlled by one (Taylor and Quisenberry, 1935) or by two recessive genes, kr_1 and kr_2 (Lein, 1943) in wheat. In contrast, dominant genes in *S. cereale* control crossability with wheat (Tanner and Falk, 1981). Therefore, interactions between the crossability genes in wheat and rye may reduce or enhance seed set in wheat-rye and rye-wheat crosses, and the use of wheat genotypes previously known to cross easily with rye should assure initial success in obtaining interspecific and intergeneric hybrids.

7D–3 HYBRID PRODUCTION

Size and plumpness of kernels, viability of hybrid embryos, and vigor of hybrid seedlings often differ in reciprocal crosses between species belonging to the same as well as different genera in Triticeae. Ploidy differences between the hybrid embryo and endosperm were assumed to cause differential seed development and embryo viability in reciprocal crosses among the diploid (2n=14; AA), tetraploid (2n=28; AABB), and hexaploid (2n=42; AABBDD) *Triticum* spp. (Boyes and Thompson, 1937). In general, polyploid species cross better as female than male, but crosses involving *T. aestivum* or *T. turgidum* L. and several diploids—*T. umbellulatum* (Zhuk.) Bowden, *T. uniaristatum* Vis., *T. longissimum* (Schwein F. & Musch.) Bowden and *T. bicorne* Forsk.—produced only shriveled and inviable seeds, even when diploids were used as males (Kihara, 1937). But reciprocal crosses with *T. turgidum* were successful (Maan, 1975). To overcome this interspecific cross-incompatibility between *T. aestivum* and *T. umbellulatum*, Sears (1956b) crossed a synthetic amphiploid of *T. turgidum* var. *dicoccoides* Körn. × *T. umbellulatum* with *T. aestivum* and obtained viable plump seeds. Similarly, Maan (1976) crossed a synthetic tetraploid *T. tauschii* Coss. as a female with *T. turgidum*, and obtained an F_1 hybrid with *T. tauschii* cytoplasm. The cross between diploid *T. tauschii* and *T. turgidum* produced only shriveled and inviable seed, even though the reciprocal cross produced viable seed and

an F_1 hybrid from which a fertile amphiploid was obtained (McFadden and Sears, 1946). Maan (1977) further demonstrated that chromosome 1D (or telocentric 1DL) was essential for the viability of embryos and seedlings of alloplasmic *T. turgidum* with *T. tauschii* cytoplasm. Thus, female gametes of the synthetic tetraploid *T. tauschii* may have contributed an optimum dose (four instead of the normal two) of the essential nuclear gene or genes to the hybrid endosperm from a cross of the tetraploid *T. tauschii* × *T. turgidum* and thereby improved embryo-endosperm as well as nucleo-cytoplasmic compatibilities.

However, certain species of *Triticum* are cross-compatible only as a male or a female with other species of *Triticum* and related genera, regardless of the ploidy differences between the parental species. Thus, *T. speltoides* Tausch. was crossable only as a female (Kihara, 1937), and *T. monococcum* L. var. *urartu* was crossable only as a male with several diploid or polyploid species of *Triticum* (Gill and Waines, 1978). These authors proposed that dosage of a genetic factor contributed by the male parent (pollen or gamete) interacted with the genome of the maternal species and thereby caused endosperm abortion in *T. monococcum* var. *urarta* (female) × *T. monococcum* var. *boeoticum* (male). The reciprocal cross produced male sterile plants of normal vigor with seven pairs of chromosomes at metaphase of meiosis in the pollen mother cells. Also, embryo-endosperm incompatibilities may be overcome by hormonal treatments and by culturing immature hybrid embryos on synthetic media (Hadley and Openshaw, 1980; Murashige, 1977).

7D–4 HYBRID STERILITY

Sterility of interspecific and intergeneric hybrids may remain an obstacle to the transfer of alien genes to wheat, even when cross-incompatibility barriers are circumvented and mature hybrids are obtained. Most sterile hybrids may be converted to fertile amphiploids by colchicine treatment of hybrid seeds or seedlings (Sears, 1941a, 1941b). Specific genotypes of certain parental species may produce hybrids with varying frequences of meiotic nonreduction, resulting in unreduced male and female gametes, and fertile amphiploid progeny with stable meiosis (Maan and Sasakuma, 1977). In general, natural or synthetic amphiploids are easier to use for the transfer of desired alien genes to wheat cultivars than sterile hybrids from direct crosses between alien species with desired genes and cultivated wheats (Morris and Sears, 1967; Kimber, 1979).

However, certain exceptional synthetic amphiploids may have unstable meiosis and a high degree of sterility as reported by Sears (1941a) in the *T. umbellulatum–Haynaldia villosa* Schur. amphiploid. Also, certain sterile F_1 hybrids may not be amenable to chromosome doubling by colchicine treatment. The F_1s of *T. aestivum* × *H. vulgare* (Islam et al., 1981), *T. aestivum* × *Agropyron trachycaulum* (Link) Malte [*Elymus trachycaulus* (Link) Gould ex Shinners], and *T. monococcum* var. *urartu*

× *T. turgidum* var. *durum*, (Gill, unpublished) could not be converted to amphiploids by repeated attempts at colchicine treatment.

7D–5 INTERSPECIFIC AND INTERGENERIC HYBRIDS

Knobloch (1968) made an extensive list of interspecific and intergeneric hybrids in the Gramineae. Species of *Triticum* were involved in 723 of the hybrids. Kimber and Abubakar (1979) compiled a list of 318 hybrids involving 47 species of *Triticum* L. and related genera *Agropyron* Gaertn., *Elytrigia* Desaux, *Secale* L., *Haynaldia* Schur., *Hordeum* L., and *Elymus* L. *Triticum aestivum*, *T. turgidum*, and *T. timopheevii* Zhuk. were involved in 86 of them. Literature on wide hybridization in Triticinae has been reviewed frequently (Percival, 1921; Leighty et al., 1926; Aase, 1930, 1946; Kihara, 1937, 1954; Sears, 1941a, 1941b, 1948, 1956a; White, 1940; Smith, 1942, 1943; Armstrong, 1936, 1945; Armstrong and McLennan, 1944; Love, 1947; Sharma and Gill, 1983b).

7D–5.1 Intra-Triticum Hybrids

Sears (1941a, 1941b, 1948, 1956a) examined fertility and meiotic chromosome pairing in the F_1s and amphiploids of crosses involving diploid *T. monococcum* and *T. bicorne* Forsk., *T. speltoides* Tausch., *T. dichasians* Zhuk., *T. umbellulatum*, *T. tauschii*, *T. comosum* Sibth & Sm., and *T. uniaristatum*. Kimber (1979) studied F_1s of *T. monococcum* × *T. longissimum* and T. monococcum × *T. tripsacoides* Jaub. & Spach. All diploid F_1s were completely self-sterile and highly female sterile. Most hybrids had none, one, or two closed bivalents per cell, and occasionally a multivalent. The *T. speltoides* × *T. monococcum* F_1s had a range of 0.38 to 2.24 closed bivalents per cell, depending on the accession of *T. speltoides* used as a parent in the cross. The generally low level of meiotic pairing between chromosomes of the diploid species indicated that their chromosomes were structurally well differentiated. The occurrence of low levels of meiotic pairing in F_1s and the presence of one or more multivalents in most amphiploids indicated that there were some residual genetic affinities between the homoeologous chromosomes of the diploid species.

Triploid hybrids involving cultivated *Triticum* spp. have been obtained by crossing *T. monococcum* with tetraploid *T. turgidum* or *T. timopheevii*, and by crossing *T. turgidum* or *T. timopheevii* with wild diploid *Triticum* spp. Meiotic chromosome pairing data from triploid hybrids provide a more reliable indication of genomic homologies between the parental diploid (2x) and tetraploid (4x) *Triticum* spp. than those from 4x × 4x or 4x × 6x or 2x × 6x combinations (Kihara, 1937; Kimber, 1979). Similarly, amphiploids of triploid hybrids are likely to be more fertile and meiotically more stable than amphiploids from crosses between species with higher ploidy levels (Kostoff, 1940; Peto and Boyes,

1940). Apparently, the potential for allosyndetic homologous pairing in the triploid F_1s and for autosyndetic homologous pairing in the synthetic hexaploid is maximized if one of the genomes in the tetraploid is closely related to the genome of the diploid parental species.

Tetraploid hybrids have been obtained by crossing 1) cultivated *T. turgidum* with *T. timopheevii*; 2) *T. turgidum* or *T. timopheevii* with wild tetraploid species, e.g., *T. triunciale* L., *T. triaristatum* Willd., *T. ovatum* L., *T. cylindricum* Ces., *T. crassum* Boiss., or *T. ventricosum* Ces.; 3) *T. monococcum* with hexaploid *T. aestivum; and 4) T. aestivum* with wild diploid species, e.g., *T. monococcum* or var. *boeoticum* Boiss., *T. longissimum*, *T. speltoides*, *T. dichasians*, *T. umbellulatum*, *T. tauschii*, or *T. comosum*. In general, octoploid amphiploids of tetraploid hybrids are likely to be less fertile and cytologically less stable than tetraploid or hexaploid amphiploids (Kostoff, 1940).

Pentaploid hybrids have been obtained by crossing 1) *T. aestivum* with *T. turgidum*, *T. timopheevii*, or wild tetraploid *Triticum* spp., and 2) *T. turgidum* (or *T. timopheevii*) with hexaploid *Triticum* spp., e.g., *T. syriacum* Bowden (DMS) or *T. triaristatum* (Willd.) Godr. & Gren. (6x).

Hexaploid hybrids have been obtained by crossing *T. aestivum* with *T. juvenale* Thell., *T. syriacum*, *T. triaristatum*, or *T. timopheevii* var. *zhukovskyi* Zhuk.

7D–5.2 Intergeneric Hybrids Involving Triticum Species

Cultivated species of *Triticum* have been successfully crossed with species of *Secale*, *Agropyron*, *Elytrigia*, *Haynaldia*, *Elymus*, and *Hordeum*. In F_1 hybrids, chromosomes of *Triticum* spp. do not pair, or pair very little with the chromosomes of the species of related genera, even though certain alien chromosomes have been shown to compensate, at least partially, for specific chromosomes of *T. aestivum*.

7D–5.2.1 Triticum–Secale Hybrids

Within species of *Triticum* and *Secale*, substantial intraspecific variability in crossability has been reported, and wheat-rye hybrids are easier to obtain than rye-wheat hybrids (Backhouse, 1916; Leighty and Sando, 1928). Most *Triticum–Secale* hybrids are completely male sterile and highly female sterile. Occasionally, fertilization involving unreduced functional gametes results in selfed seed that produces fertile amphiploid progeny. The chromosomes of *Triticum* spp. do not pair with chromosomes of *Secale* spp., and meiosis in the F_1 is highly irregular.

7D–5.2.2 Triticum–Agropyron (Elytrigia) Hybrids

There are approximately 100 species of *Agropyron* (including *Elytrigia*); about 30 have been crossed with species of *Triticum* (Smith, 1942). Several workers have reviewed the early literature on *Triticum–Agro-*

pyron and *Triticum–Elytrigia* hybridization (White, 1940; Smith, 1942, 1943; Armstrong, 1945; Love, 1947; Sharma and Gill, 1983b). Sears (1948) concluded that the chromosomes of *Triticum* spp. do not pair with the chromosomes of *Agropyron* (including *Elytrigia*) spp. According to Love (1947), *Agropyron elongatum* (Host) Beauv. [*Elytrigia pontica* (Podp.) Holub] (2n=70) and *A. intermedium* (Host) Beauv. (*A. glaucum* Desf.) (2n=42) [*E. intermedia* (Host) Nevski] were more frequently used in crosses with wheat than other *Agropyron* or *Elytrigia* spp. and were more easily crossable with tetraploid *T. turgidum* and hexaploid *T. aestivum* spp. Seed was more plump from *T. turgidum* × *A. intermedium* or *T. aestivum* × *A. elongatum* crosses than from *T. turgidum* × *A. elongtum* or *T. aestivum* × *A. intermedium* crosses. Most workers were unable to cross *A. repens* (L.) Beauv. [*E. repens* (L.) Nevski] with *Triticum* spp., but Tsitsin (1936) reported that certain forms of *A. repens* crossed easily with wheat. Also, Tsitsin (1933) crossed *A. elongatum and A. intermedium* with *T. monococcum*, and *A. trichophorum* (Link) Rieht [*E. intermedia* ssp. *barbelato* (Schur.) A. Love] (2n=42) and *A. junceum* (L.) Beauv. [*E. juncea* (L.) Nevski] (2n=28) with both tetraploid and hexaploid species of *Triticum*. Veruschkine (1936) crossed *A. elongatiforme* Drob. [*E. elongatiformis* (Drob.) Nevski] with wheat, and *A. cristatum* (L.) Gaertn. with *T. timopheevii*.

Crossability and fertility of *T. aestivum* × *A. elongatum* F_1 hybrids largely depended on the specific genotypes of parental species used in hybridization experiments. In crosses with *Triticum* spp., most other *Agropyron* and *Elytrigia* spp. produced completely male sterile and highly female sterile F_1 hybrids. However, Tsitsin (1936) reported selfed seed set on F_1s of *T. aestivum* × *A. intermedium*, and Khiznjak (1937) reported selfed seed set on F_1s of tetraploid species of *Triticum* × *A. intermedium*.

Sharma and Gill (1983a) produced hybrids of *T. aestivum* with *A. trachycaulum* (*E. trachycaulus*), *A. ciliare* (Trin.) Franchet [*Elymus ciliaris* (Trin.) Tzveler], *A. yezoense* Honda (*Elymus yezoensis* Honda), *A. scirpeum* (K. Prese [*Elytrigia scirpea* (K. Prese) Holub], *A. junceum*, and *A. intermedium*. Muramatsu et al. (1983) produced hybrids of four Japanese indigenous *Agropyron* spp., *A. tsukushiense* (Honda) Ohwi (*Elymus tsukushiensis* Honda) (2n=42), *A. humidorum* (2n=42), *A. ciliare* (Trin.) Franchet (2n=28), and *A. yezoense* (2n=28), with *T. aestivum*, by incubation of immature hybrid embryos on synthetic culture media.

7D-5.2.3 Triticum–Hordeum Hybrids

Five species of *Hordeum* have been successfully crossed with species of *Triticum*. Most hybrids, except *T. timopheevii* × *H. bogdanii* Wil. (Kimber and Sallee, 1976), were obtained by treatment of emasculated florets with gibberellic acid before or after pollination, and by use of embryo culture on synthetic media. In general, F_1 hybrids were completely self-sterile and partially female fertile, and were not easily amenable to chromosome doubling (amphiploidy) by colchicine treatment

(especially those involving *H. vulgare*). So far three amphiploids have been obtained, *T. turgidum* × *H. chilense* (Martin and Laguna, 1980), *T. timopheevii* × *H. bogadanii* (Kimber, 1979) and *T. aestivum* × *H. chilense* (Chapman and Miller, 1978).

The chromosomes of *Triticum* spp. did not pair, or paired very little, with the chromosomes of *Hordeum* spp. in the F_1s of *T. timopheevii* × *H. bogdanii* (Kimber and Sallee, 1976), *H. chilense* × *T. turgidum* (Martin and Laguna, 1980), *H. chilense* × *T. aestivum* (Martin and Chapman, 1977), *H. chilense* × *T. tauschii* (Martin, 1983), and *H. pusillum* Nutt. × *T. aestivum* (Finch and Bennett, 1980). Similarly, Padilla and Martin (1983) reported no meiotic pairing between the chromosomes of *H. chilense* and six tetraploid *Triticum* spp. and subspecies (*T. timopheevii*, *T. turgidum* ssp. *dicoccoides*, *georgicum, carthlicum, turanicum*, or *poloncum*).

Islam et al. (1981) examined F_1 hybrids from reciprocal crosses between *T. aestivum* and *H. vulgare* and developed disomic addition lines of *T. aestivum* with individual chromosomes of *H. vulgare*. Miller et al. (1982) obtained wheat addition lines with *H. chilense* chromosomes.

7D-5.2.4 Triticum–Haynaldia Hybrids

Haynaldia villosa Schur has been successfully crossed with *T. monococcum* (Sando, 1935; Sears, 1948), *T. turgidum* (Tschermak, 1930; Kostoff and Arutiunova, 1937), *T. timopheevii*, and *T. aestivum* (Kostoff and Arutiunova, 1937). Amphidiploids of *T. monococcum–H. villosa* (Sears, 1948), *H. villosa–T. turgidum* (Zhukovsky, 1972, Leningrad, personal communication) and *T. turgidum–H. villosa* (Kostoff and Arutiunova, 1937; Tschermak, 1930) have been obtained. *Triticum–Haynaldia* F_1s are completely male sterile and partially female fertile. *Triticum* chromosomes do not pair with *Haynaldia* chromosomes in the F_1 hybrids.

7D-5.2.5 Triticum–Elymus Hybrids

Mujeeb-Kazi and Rodriguez (1981) obtained hybrids between *T. aestivum* × *Elymus giganteus* Vahl (*Laymus racemosus* (Lam.) Tzveler. Thomas et al. (1981) reported crossing *T. tauschii* with *E. arenarius* L.

7D–6 CONCLUSION

For more than a century, steady progress has been made in the development of methods to produce new hybrids and amphidiploids from wide crosses between species of *Triticum* and related genera which previously had been considered to be cross-incompatible. A few new hybrids are being added to the list each year. As a result, substantial progress has been made in (i) establishing phylogenetic relationships among the species and genera in Triticeae, identifying diploid progenitors of the polyploid

species, and producing new amphidiploids, and (ii) analysis of genetic isolating mechanisms between species, hybrid embryo and endosperm, and nuclear and cytoplasmic genes.

There are several areas of research where future attention may be directed to improve genetic diversity of the wheat crop. To assure success, it is imperative that well-funded, long-range, cooperative programs be established for:

1. The evaluation of available genetic diversity and the identification of superior genetic stocks for specific desirable alien traits to improve productivity and to make wheat less vulnerable to present and future pests and environmental hazards.
2. The investigation of interspecific and intergeneric isolating mechanisms which act as barriers to genetic transfers between species. Since chromosomes of cultivated species of *Triticum* do not meiotically pair (or pair very little) with the chromosomes of related genera in intergeneric hybrids, it is desirable that new methods be developed to induce the transfer of desirable genes from alien species to wheat chromosomes.

7E Transferring Alien Genes to Wheat

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In broad terms an alien gene can be considered to be any gene transferred to wheat from a related species. As described above by Maan (section 7D) the genus *Triticum* contains a broad range of species, some of which cross readily with the cultivated tetraploid (*T. Turgidum* L.) or hexaploid (*T. aestivum* L.) wheats, and others only with great difficulty. In addition, wheat will also cross with species in a number of other genera including *Agropyron, Elymus, Elytrigia* (=*Agropyron*), *Haynaldia, Hordeum*, and *Secale* (Riley and Kimber, 1966; Knobloch, 1968; Feldman and Sears, 1981). In discussing the *Triticum* and *Aegilops* spp., the classification by Kimber and Sears, section 5A–1, above, will be followed. For the *Agropyron* and related species the classification described by Dewey (1983) will be used. To avoid confusion, in referring to the literature the designations used by the authors will be given, followed by the new designation.

The wild relatives of wheat are adapted to a broad range of environments and carry a large reservoir of useful genes (Zohary et al., 1969; Kerber and Dyck, 1973; Brezhnev, 1977; Feldman and Sears, 1981; Limin and Fowler, 1981; Sharma et al., 1981; McGuire and Dvorak, 1981). Initially they were considered to be primarily sources of disease resistance, but more recently they have been recognized as potential sources of genes for high protein, cold tolerance, salt tolerance, drought tolerance, lodging resistance, early maturity, and even yield. Extensive screening of the wild relatives of wheat needs to be done before their useful genes can be fully utilized.

When species carrying useful genes have been identified, the next step is to transfer the genes to wheat. The success of the transfer depends on several factors: the difficulty in making the cross (see section 7D above), the amount of pairing that occurs between the alien chromosome(s) and wheat chromosomes (the A,B, or D genomes), and the genetic complexity of the character. On the basis of chromosome pairing, alien transfers to

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wheat can be divided into two categories: transfers between homologous chromosomes and transfers between nonhomologous but often homoeologous chromosomes. The genomic formulae of wheat and its relatives are given in section 5A. In a species carrying one genome that is homologous to a wheat genome and one or more genomes that are homoeologous, the transfer can be in either category, depending upon which genome carries the gene (or genes). If several genes are involved, it is possible that both homologous and homoeologous transfers will be required. Kimber (1984) points out that genome relationships must be clearly understood before the appropriate technique for introduction of alien variation into wheat can be selected.

7E–1 TRANSFERS BETWEEN HOMOLOGOUS CHROMOSOMES

7E–1.1 Transfers Between Tetraploid and Bread Wheats

The transfer of genes to bread wheat (*T. aestivum* AABBDD) from the tetraploid durum and emmer wheats (*T. turgidum* AABB) is relatively simple. Hybrids are easily made, fairly fertile, and readily backcrossed to bread wheat. Usually, bread wheat is used as the female parent. However, Grama and Gerechter-Amitai (1974) found that in transferring stripe rust (*Puccinia striiformis* West) resistance from *T. dicoccoides* (*T. turgidum*) G-25 to bread wheat, seed set was obtained only when *T. aestivum* was used as the male. In early work of this type, Hayes et al. (1920) transferred rust resistance from 'Iumillo' durum to 'Marquillo', a parent of the very important cultivar Thatcher. Similarly, McFadden (1930) transferred rust resistance from 'Yaroslav' emmer to the bread wheats 'Hope' and 'H44,' both of which have been widely used as parents.

Even in crosses of this type, the transfer will involve a block of genes which may not be readily separated by crossing over. Some of the genes may be deleterious. For example, when stem rust resistance was transferred from 'Gaza' durum to 'Bobbin' bread wheat, a pollen-killer gene was also transferred (Loegering and Sears, 1963). Often genes for characters such as tenacious glumes are transferred as well.

An even greater problem may be the failure of genes to be expressed when transferred from a tetraploid to a hexaploid. Kerber (1983) failed in repeated attempts to transfer leaf rust (*Puccinia recondita* Rob. ex. Desm.) resistance from 'Stewart 63' durum wheat to 'Canthatch' and 'Marquis' bread wheat. An amphiploid between Stewart 63 and *T. tauschii* (Coss.) Schmal. (DD) was susceptible to leaf rust, indicating that the D genome carries a suppressor of resistance. Similarly, Kerber and Green (1980) showed that chromosome 7DL of the bread wheat cultivar Canthatch carries a suppressor of resistance to stem rust (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn.). Kerber (1983) tested six bread wheat

cultivars and six synthetic hexaploids (AABBDD) and found that they all possessed the same suppressor of resistance.

The reverse transfer of genes from bread wheat to durum wheat is possible if the genes are in the A or B genomes, but has seldom, if ever, been reported. However, Kerber (Agriculture Canada Research Station, Winnipeg, 1984, personal communication) did transfer the gene *Sr7a* for stem rust resistance from bread to durum wheat.

7E–1.2 Transfers from Einkorn to Bread Wheat

Einkorn wheats (*T. monococcum* L. AA) cross readily with bread wheat, but the hybrid embryos differ greatly in the ease with which they can be cultured. Transfers can be made most readily by crossing first to a durum wheat. The F_1 hybrid can be either crossed with bread wheat or backcrossed once or twice to the durum wheat and then crossed to a bread wheat. As Kerber and Dyck (1973) discovered, some crosses between einkorn and durum wheats are compatible while others are not. For example, an einkorn line, RL5244, was compatible with the durum cultivar Stewart but not with 'Arnautka'. In transferring stem rust resistance from einkorn to bread wheat, several authors have noted a progressive loss of resistance (Kerber and Dyck, 1973, Knott, 1979). For example, Kerber and Dyck (1973) reported an infection type 0;1 in a diploid, and type 1^+ in the tetraploid and type 2 in the hexaploid derived from it.

7E–1.3 Transfers from *T. tauschii* to Bread Wheat

Crosses between *T. turgidum* and *T. tauschii* (DD) have frequently been made and the hybrid doubled to produce synthetic hexaploid wheats. When the synthetic hexaploids are crossed with bread wheat, chromosome pairing in the hybrids is usually good. Kerber and Dyck (1969) and Dyck and Kerber (1970) identified good resistance to leaf rust in *Aegilops squarrosa* (= *T. tauschii*) and transferred two genes for seedling resistance and one gene for adult plant resistance to bread wheat. The latter was closely linked to a gene for tenacious glumes (nonfree threshability).

Joppa et al. (1980) produced a synthetic hexaploid between *T. turgidum* and *T. tauschii* and showed that it had a single dominant gene for resistance to greenbug (*Schizaphis graminum* Rondani) toxin. Martin et al. (1982) used synthetic hexaploids produced by Tanaka to develop wheats with resistance to both Hessian fly [*Mayetiola destructor* (Say)] and greenbug.

Genes also can be transferred from *T. tauschii* by crossing it with *T. aestivum* and backcrossing to *aestivum* one or more times (Merkle and Starks, 1985).

Since the D genome of *T. tauschii* is responsible for the breadmaking properties of bread wheat, it is a potential source of additional genes for breadmaking quality.

7E–2 TRANSFERS FROM SPECIES WITH ONE GENOME HOMOLOGOUS TO A WHEAT GENOME

The difficulty in making transfers from species with one genome homologous to a wheat genome depends partly on whether the gene is on a chromosome homologous with a wheat chromosome. The most extensive work has been done with *T. timopheevii* (Zhuk.) Zhuk. (AAGG) and *T. ventricosum* Ces. (DDUnUn).

Triticum timopheevii is noted for its disease resistance, and a number of attempts have been made to transfer its resistance to various diseases to bread wheat. Originally it was thought that *T. timopheevii* carried an A genome plus a modified B genome, but it is now generally agreed that it has a distinct genome designated G. Like *T. turgidum*, *T. timopheevii* can be crossed fairly readily with *T. aestivum*. The best seed is obtained when *timopheevii* is used as the male parent. However, the hybrids with *timopheevii* are much less fertile than those with *turgidum*, although seeds can usually be obtained in backcrosses to the bread wheat parent. Male sterility often continues to be a problem even after one or more backcrosses. Nevertheless, several transfers have been made. Allard and Shands (1954) transferred resistance to stem rust, leaf rust, and powdery mildew (*Erysiphe graminis* D.C. f. sp. *tritici* E. Marchal). Their studies indicated that resistance to stem rust was controlled by two linked genes and that mildew resistance was closely associated with rust resistance. However, when Nyquist (1962) crossed the resistant derivative, CI 12633, with five susceptible cultivars, he obtained a range from 7.1 to 26.6% of stem rust susceptible plants in the F_2 populations. He concluded that differential fertilization was at least partially responsible and that only one gene for resistance was involved. This gene, *SrTtl*=*Sr36*, has been used in several Australian cultivars such as 'Timvera' and 'Mengavi'. Maan and McCracken (1968) found that bread wheat strains derived from *T. timopheevii* crosses tended to show meiotic irregularities.

McIntosh and Gyarfas (1971) studied 22 accessions of *T. timopheevii* and three *T. aestivum* lines carrying genes for stem rust resistance from *timopheevii*. Their data indicated that *T. timopheevii* carries genes for resistance in addition to the three already transferred.

Triticum timopheevii can also be used as a source of disease resistance in durum wheat, as shown by Deodikar et al. (1979).

Aegilops ventricosa Tausch (=*T. ventricosum* Ces.) carries a D genome plus the genome Un. Thus, one genome will pair with a wheat genome and one will not. Sprague (1936) found that *Ae. ventricosa* has good resistance to eyespot, *Cercosporella herpotrichoides* Fron. Similarly, Dosba and Doussinault (1977) tested eight diploid and tetraploid *Aegilops* (=*Triticum*) species and found that only *Ae. ventricosa* and one line of *Ae. squarrosa* (=*T. tauschii*) had good resistance to eyespot.

Three methods of transferring resistance from *Ae. ventricosa* have been attempted (Delibes et al., 1977): (i) direct hybridization between *Ae.*

ventricosa and *T. aestivum* (the cross is generally unsuccessful, but Dosba and Cauderon [1972] reported obtaining two plants which were male sterile but gave 12 seeds in a backcross with *T. aestivum*); (ii) crossing *Ae. ventricosa* with *T. turgidum* and then crossing the hybrid (ABDUn) with *T. aestivum*; and (iii) producing an amphidiploid (AABBDDUnUn) from the cross between *Ae. ventricosa* and *T. turgidum*, and crossing it to *T. aestivum*. Both methods (ii) and (iii) have been used successfully by several workers. Using method (ii), Dosba and Doussinault (1977) obtained lines with good resistance and assumed that the resistance came from the D genome. However, by testing chromosome addition lines, they showed that at least one Un chromosome was involved in resistance. *Aegilops ventricosa* cytoplasm also promoted resistance. Doussinault et al. (1983) screened lines from crosses with *ventricosa* for biochemical markers carried on the D and Un genome chromosomes. Markers on the D chromosomes appeared in 30 to 60% of the plants, while those on the Un chromosomes were present in $< 4\%$. The Un chromosomes carry genes for other useful characters, and attempts are being made to transfer them by promoting homoeologous recombination.

7E–3 TRANSFERS INVOLVING HOMOEOLOGOUS CHROMOSOMES

Many of the more distant relatives of wheat which do not carry an A, B, or D genome appear to have many useful characters, particularly disease, insect, and stress resistance. Various methods of transferring characters from these species to wheat have been developed.

7E–3.1 Development of Amphiploids and Addition and Substitution Lines

In most transfers, the first step is the production of suitable stocks in which to induce translocations or crossing over between homoeologous chromosomes. Many alien species have been crossed with either durum or bread wheat and the chromosome number of the F_1 hybrid doubled with colchicine to produce an amphiploid (Riley and Kimber, 1966). When the alien species does not carry a genome homologous with one in the wheat parent, the amphiploids normally behave as allopolyploids and show mostly bivalents and few if any multivalents at meiosis. Thus, no exchange between alien and wheat chromosomes will occur.

Many transfers of interest to plant breeders involve simply inherited characters such as disease and insect resistance. In these cases it is common to develop an addition or substitution line carrying the chromosome on which the desired gene is located. This can be done by crossing the alien species with wheat and crossing either the polyhaploid F_1 plants or the amphiploid with the wheat parent. Selection for the desired character through several backcrosses followed by selfing will result in the pro-

duction of an addition line. Occasionally, natural substitutions of an alien chromosome for a wheat chromosome will occur. Usually these substitutions have been found to involve homoeologous chromosomes.

Substitutions can also be produced by crossing a specific wheat monosomic line with an addition line. The progeny will be either $21''+1'A$ (A=alien chromosome) or $20''+1'W+1'A$ (W=wheat chromosome). From selfing the latter plants, both additions and substitutions should be produced, particularly if the alien chromosome is homoeolgous to the missing wheat chromosome.

One alternative procedure is to use the $20''+1'W+1'A$ plants as males in a cross to the original monosomic line. If the alien chromosome substitutes well for the wheat chromosome, $20''+1'A$ pollen will function and $20''+1'A$ plants will be produced. These can then be selfed to produce the disomic substitution.

A second alternative is to pollinate $20''+1'W+1'A$ plants by the parental addition line. Since no selection against the alien chromosome is expected in the female, about three-eighths of the progeny should be $21''+1'$, and half of these should be $20''+1''A+1'W$. The substitution line should then be relatively easily obtained by selfing, even if male transmission of the alien chromosome is poor (Sears, Department of Agronomy, University of Missouri, Columbia, 1985, personal communication).

An alien addition monosome tends to misdivide so that telosomic additions are often obtained. An alien telosome has the advantage that it can easily be identified cytologically and its pairing frequency determined (Sears, 1981). However, when a telosome pairs with a normal chromosome, crossing over tends to be shifted distally and this may or may not be advantageous.

Addition lines are often reasonably vigorous but tend to be unstable. Any failure of pairing of the alien chromosomes at meiosis can result in a normal wheat gamete which will probably have a competitive advantage over an addition gamete. Thus the alien chromosome will tend to be lost.

Endo (1982) reported that specific chromosomes of three *Aegilops* (*Triticum* spp. had gametocidal action when added to bread wheat. Both male and female fertility were reduced and most functional gametes carried the *Aegilops* chromosome. Tsujimoto and Tsunewaki (1984) reported the integration of a gametocidal gene from an *A. speltoides* chromosome into a wheat chromosome.

The vigor of substitution lines depends on the degree of compensation by the alien chromosome for the wheat chromosome. Often only homoeologous substitutions are possible and the lines may be essentially normal in vigor. Pairing is usually normal in substitution lines but, even if the alien chromosomes fail to pair, loss of a chromosome results in an n-1 gamete that is likely to be noncompetitive, particularly in the pollen. Substitution lines, therefore, tend to be stable and have some potential as commercial cultivars. A number of European wheat cultivars have resistance to stem, leaf, and stripe rust, and to powdery mildew, as a

result of the substitution of rye (*Secale cereale* L.) chromosome 1R for wheat chromosome 1B (Mettin et al., 1973, and Zeller, 1973).

7E–3.2 Spontaneous Translocations

Occasionally in wide crosses spontaneous translocations occur between alien and wheat chromosomes. Several European wheat cultivars carry a spontaneous 1B/1R translocation (Mettin et al., 1973; Zeller, 1973). Similarly, a spontaneous translocation involving chromosome 3D occurred in the production of the leaf and stem rust resistant cultivar Agent from a cross involving a wheat–*Agropyron elongatum* derivative (Smith et al., 1968). Resistance derived from Agent has been used in a number of U.S. cultivars. Virulence has appeared in the field for the leaf rust resistance gene *Lr24*, but not for the stem rust resistance gene *Sr24*.

Sears (1972) proposed a method of transferring genes involving the exchange of whole chromosome arms. In plants that are $20'' + 1'W + 1'A$, the univalents occasionally misdivide at meiosis. If both misdivide in the same cell, a wheat chromosome arm may rejoin with an alien chromosome arm. However, the frequency is so low that the method may be relatively impractical (Sears, 1981). Nevertheless, Zeller (1981) reported the production of two wheat-rye exchanges, using crosses between 'Chinese Spring' monosomics and Chinese Spring–rye addition lines.

Jan et al. (1981) produced a spontaneous translocation involving an *Elytrigia* chromosome carrying a gene for blue aleurone. An exchange of chromosome arms was probably involved.

7E–3.3 The Use of Ionizing Radiation to Produce Translocations

Sears (1956b) developed a method using ionizing radiation to produce translocations between a wheat chromosome and an alien chromosome from *Ae. umbellulata* (*T. umbellulatum* UU) carrying a gene for resistance to leaf rust. Wheat plants carrying a monosomic addition of the *umbellulata* chromosome were produced. Sears then irradiated monoisosomic addition plants with x-rays prior to meiosis and used their pollen on susceptible wheat plants. Leaf rust resistant progeny were examined cytologically and plants carrying translocations were identified. The resistance of one line, designated Transfer (*Lr9*), was used in several cultivars in the United States but was quickly overcome by the pathogen.

Other workers have used similar procedures to transfer rust resistance from rye and *Agropyron* spp. to wheat (see Knott, 1971, for a review). Both plants and seeds have been irradiated with various types of radiation including x-rays, gamma rays, and neutrons. However, the procedure is laborious and the probability of obtaining useful translocations is low, since most will involve non-homoeologous chromosomes and have deleterious effects. Translocations frequently show reduced transmission through the gametes, particularly the pollen. With the development of methods for inducing homoeologous pairing, the use of radiation has

largely been superseded. In the future it is likely to be useful only if induced homoeologous pairing with an alien chromosome is so low in frequency as to be unusable.

Relatively little use has been made of radiation-produced translocations in commercial cultivars. However, the stem rust resistance transferred from *A. elongatum (Elytrigia pontica)* by Knott (1961) has been used extensively in Australian cultivars and so far has proven to be durable (Driscoll 1981).

7E–3.4 Transfers Using Induced Homoeologous Pairing

The discovery of the genetic control of chromosome pairing in wheat (Okamoto, 1957, Riley, 1958) made possible the development of more effective methods for transferring genes from alien chromosomes. Homoeologous pairing is controlled by the interaction of genes on several chromosomes, but the major suppressor of pairing, *Ph1*, is on chromosome 5B. Three basic types of procedure have been developed to induce pairing between homoeologous wheat and alien chromosomes: (i) the production of plants lacking *Ph1*; (ii) the use of crosses with species carrying a suppressor of *Ph1*; and (iii) the use of a *ph* mutant.

7E–3.4.1 Production of Plants Lacking Ph1

The simplest way of producingg wheat × alien species crosses that lack *Ph1* is to pollinate a wheat plant monosomic for chromosome 5B with pollen from the alien species. Homoeologous pairing should occur in the F_1 plants which lack 5B and are monosomic for the alien chromosome. As long as the latter are at least female fertile in a backcross to wheat, the crossover chromosomes can be recovered. Riley (1966) used this procedure to transfer genetic material from *Ae. bicornis* Forsk. Jaub. & Spach. (*T. bicorne*) to wheat. Joshi and Singh (1979) crossed monosomic 5B of 'Pb.C591' × 'Russian' rye. No 27-chromosome plant was obtained, but one with 28 chromosomes showed extensive pairing, suggesting that it carried a mutant *ph1* or was nullisomic for 5B and disomic for another wheat chromosome. Following two backcrosses to Pb.C591, plants with resistance to all three wheat rusts were obtained.

The nullisomic-5B tetrasomic-5D line developed by Sears (1966) can be used to produce plants lacking chromosome 5B. One procedure is to cross monosomic 5B × an alien substitution line (e.g., a line with an *Agropyron* chromosome carrying a gene for stem rust resistance substituted for chromosome 7D). About three-quarters of the progeny should be 19″+1′5B+1′7D+1′Ag. These plants are selected and pollinated by nulli-5B tetra-5D. Progeny that are rust resistant and show multivalent pairing (lacking 5B) are selected and then crossed and backcrossed to bread wheat. Plants in which homoeologous crossing-over has transferred the rust resistance to a wheat chromosome should be obtained.

Sears (1973) used this procedure to transfer leaf rust resistance to

wheat from two wheat– *Agropyron* derivatives, 'TAP 67', the source of the resistance in Agent, and 'Agrus', the source of the resistance in 'Agatha'. Despite the fact that homoeologous crossovers were involved, in each case several of the lines showed reduced transmission of the resistance through the pollen. Surprisingly, several others showed more than the normal 50% transmission. Sears (1973) found that the transfers involved substantial segments of the *Agropyron* chromosomes.

Larson (unpublished) used the nullisomic-5B tetrasomic-5D procedure to transfer resistance to the mite vector of wheat streak mosaic from *Ag. elongatum* (*Elytrigia pontica*) to bread wheat (Whelan et al., 1983).

The low fertility of the triple monosomic plants is a problem in this procedure, particularly if the frequency of homoeologous pairing involving the alien chromosome is low.

7E–3.4.2 Crosses with Species Carrying a Suppressor of Ph1

In crosses with wheat, certain strains of *Ae. speltoides* (*T. speltoides*) and *Ae. mutica* (*T. tripsacoides*) have been found to inhibit the effect of *Ph1*. Hybrids between these species and wheat can be obtained using embryo culture, and can then be backcrossed to wheat. In this way direct transfers of genetic material from *speltoides* and *mutica* to wheat can be made. Dvorak (1977) used the procedure to transfer leaf rust resistance from five accessions of *Ae. speltoides* to wheat. Of 11 lines that had been backcrossed four or five times to either 'Manitou' or 'Neepawa', four showed some promise in agronomic and quality characteristics (Knott and Dvorak, 1981).

Aegilops speltoides and *Ae. mutica* can also be used to transfer genes from other species to wheat. An alien addition line carrying the desired gene is crossed with *Ae. speltoides* and homoeologous pairing will occur in the hybrid. The hybrid is crossed and backcrossed several times to wheat with selection for the desired character in each generation. Low fertility in the hybrid may be a problem. Riley et al. (1968) used this method to transfer stripe rust resistance from Ae. comosa (*T. comosum*) to wheat. Since genetic material may be transferred from both *Ae. speltoides* and the second alien species, it may be necessary to ensure that the line of *Ae. speltoides* that is used does not carry the character that is to be transferred from the second species.

7E–3.4.3 The Use of ph Mutants

Three *ph* mutants, *ph1b* and two at the *Ph2* locus on chromosome 3D, are available in bread wheat and can be used to induce homoeologous pairing. Wall et al. (1971) produced a mutant which results in an intermediate level of homoeologous pairing. Sears (1984) showed that it is an allele of *Ph2*. Sears (1977, 1982) obtained two mutants, *ph1b*, which is apparently a deletion of *Ph1* on chromosome 5B, and *ph2a*, which has an effect similar to Wall et al.'s mutation *ph2b* and, like *ph2b*, is appar-

ently a deficiency for *Ph2*. Giorgi (1978) induced a *ph1* mutant in durum wheat, presumably also a deletion of *Ph1*.

Since the *ph* mutants are recessive, it is necessary to produce crosses in which they are either homozygous or hemizygous. To use one of the mutants, e.g., *ph1b*, the best procedure probably is to start with a line in which the alien chromosome is substituted for a homoeologue, and cross it to a monosomic 5B female. About three-fourths of the progeny should be $19''+3'$, where the univalents are 5B, the alien chromosome, and its wheat homoeologue. These plants are then crossed with the *ph1b* mutant line. In the progeny, plants are selected that show the character carried on the alien chromosome and have homoeologous pairing. They should have either 42 chromosomes, including the 5B chromosome carrying *ph1b* and the alien chromosome, or 43 chromosomes, including the 5B chromosome carrying *ph1b*, the alien chromosome, and its wheat homoeologue. The latter type is the more desirable, since the alien chromosome and its homoeologue have no homologues with which to pair and should pair with one another.

Liang et al. (1979) used this procedure to transfer wheat streak mosaic resistance from an *Agropyron intermedium* (*Elytrigia intermedia*) chromosome to wheat. Kibirige-Sebunya and Knott (1983) used both the *ph1b* mutant and nullisomic-5B tetrasomic-5D to transfer stem rust resistance from an *Ag. elongatum* (*Elytrigia pontica*) chromosome to wheat. Both the *Agropyron* chromosome involved and the recombinant chromosomes showed preferential transmission through the female gametes. This apparently resulted from a gametocidal effect such that in heterozygotes many female gametes not carrying the *Agropyron* segment failed to function.

7E–4 TRANSFER OF QUANTITATIVE CHARACTERS

Although most transfer from alien species to wheat have involved simply inherited characters, there has been increasing interest in alien species as sources of quantitative characters which are presumably more complex in inheritance. Since transfers of such characters will involve several genes, they will be increasingly difficult the more distantly related the alien species is to wheat. However, as Riley (1966) showed with *Ae. bicornis*, it is possible to transfer to wheat genetic material that affects a variety of qualitative and quantitative characters. Furthermore, although some transferred alien chromosome segments carrying genes with qualitative effects have been shown to have linked deleterious genes, others may prove to carry desirable genes for quantitative characters.

7F Novel Approaches to Wheat Improvement

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Despite many successes in agriculture, new approaches that may contribute to increased agricultural production in the future must be emphasized. This section will cover haploid production, callus induction and regeneration using immature embryos and other source tissues, and N_2 fixation by bacteria in association with roots of wheat.

7F–1 INDUCTION OF HAPLOIDS

Four major approaches to obtaining haploids in wheat ($2n=3x=21$) have been reported.

7F–1.1 Anther Culture

7F1.1.1 General Procedures

Spikes are collected when pollen grains in central florets are uninucleate (G_2 period). The whole spike is surface-sterilized with 60% ethanol or 1.7% hypochlorite solution in a laminar-flow hood. Anthers are usually removed immediately from the florets and placed on a medium. They should not be squeezed or injured since an injured anther wall can form a diploid callus. Alternatively, the spikes can be wrapped in aluminum foil and kept at 4 to 6 °C for a period of 1 to 7 days before dissecting out the anthers.

Callus-induction nutrient media are of two basic types, potato and chemically defined. The potato medium contains boiled potato extract (200 g L^{-1}) supplemented with sucrose, hormones, and iron. The com-

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position of the chemical or synthetic medium was described by Hu et al. (1978) and Liang et al. (1982). Approximately 25 mL of sterilized medium is poured into a 50-mL Erlenmeyer flask, a test tube with an aluminum or plastic slip-on cap, or a petri dish. Twenty-five to 30 anthers are placed on the medium in each flask or dish.

Cultural environments vary with researchers. Schaeffer et al. (1979) cultured anthers in the dark at 4 to 5 °C for 64 h, then increased the temperature to 26 °C for 5 days before exposing them to light (1.5 μE m^{-2} s^{-1}). Liang et al. (1982) kept anthers at low temperature (5 °C) in the dark for 7 days and then transferred the flasks to an incubation chamber at 26 °C in the dark until calli formed.

Calli can be observed about 21 days after inoculation. However, unlike tobacco (*Nicotiana tabacum* L.) where haploid seedlings are formed directly, transfer of calli to a regeneration medium is necessary in wheat (Hu et al., 1978; Schaeffer et al., 1979; Liang et al., 1982). A photoperiod of 10 to 14 h and a temperature of 24 to 29 °C is necessary for regeneration. At the 2- to 3-leaf stage, seedlings with roots are transferred to moist vermiculite in pots and covered with a translucent plastic box to prevent desiccation. The seedlings should be kept under cool temperature (20 °C) and low light intensity (1.5 μE m^{-2} s^{-1}) until they start to grow vigorously. Chromosome doubling is usually done by treating the growing points for 5 to 8 h with a solution of colchicine (0.2%) and dimethyl sulfoxide(C_2H_6OS) (DMSO, 1.5%) at a pH of 5.5.

7F-1.1.2 Pollen Mitoses

Irregular pollen mitoses that result in cells with two nuclei with no cell wall between them occur at a low and variable frequency. Sometimes vegetative pollen nuclei undergo a supernumerary division. Thus, the pollen population may be trimorphic. The abnormal pollen is smaller than normal and lacks cytoplasmic staining ability due to low RNA and protein content (Chu et al., 1978; Dunwell, 1978; Zhou, 1980).

In vivo, the frequency of abnormal pollen varies among cultivars; in vitro, the frequency increases as amount of time in culture increases (Table 7F–1). However, the relationship between abnormal types of pollen and the development of haploids is not clear.

7F-1.1.3 Callus Induction and Plantlet Regeneration

7F-1.1.3.1 Effect of Genotype. On a given medium, certain genotypes respond, produce calli, and regenerate; others do not. Using MS medium (Murashige and Skoog, 1962) supplemented with casein hydrolysate, coconut milk, (2,4-dichlorophenoxy) acetic acid ($C_8H_6Cl_2O_3$) (2,4-D) and kinetin, only one cultivar among 66 sampled produced haploid plantlets (Heszky and Mesch, 1976). Since androgenesis is genotype dependent, the response of anthers to culture must be under genetic control (Liang et al., 1982; Schaeffer et al., 1979). The response of F_1s tends to be comparable to that of their better parents and reciprocal F_1s may not

Table 7F-1. Relationship between culture period and frequency of abnormal pollen in a wheat line (7721). Source: Zhou, 1980.

Period of culture (h)	Culture medium	No. of pollen examined	Normal pollen		Abnormal pollen with 2 equal nuclei		Abnormal pollen with dividing vegetative nucleus	
			no.	%	no.	%	no.	%
48	N_6	2452	2390	97.5	62	2.5	0	0
104	N_6	1588	1036	65.2	134	8.4	418	26.3
120	N_6	3426	1923	56.0	137	4.0	1376	40.0

differ significantly (Bullock et al., 1982). However, exceptions are known: F_1 response can fall below the level of the good parent (Shimada, 1981), and crosses and reciprocal crosses can differ in the frequencies of callus formation and regeneration (Wang et al., 1978).

Genotype dependency implies that doubled haploid plants may not provide a complete representation of the gametic array produced by heterozygous plants. Bullock et al. (1982) and Zeng (1983) found that segregation ratios of the regenerated plantlets in the H_2 generation (equivalent to an F_2) tended to deviate significantly from the expected ratios.

7F-1.1.3.2 Effect of Media. Culture media consist of a basal component (organic and inorganic constituents) plus a hormone component which is critical for initiation of cell growth. The composition of a culture medium is the main factor in the induction of callus and the control of development of plantlets from microscopes. In a potato medium, a high sucrose concentration (9 to 10%) is more effective than a low one in increasing the osmotic pressure to the level essential for callus formation. However, in a synthetic medium such as N_6, a reduced concentration of NH_4^+ ions appears to be more effective than high concentrations in inducing callus formation (Hu et al., 1978). When anthers of 'Chinese Spring' wheat were placed on RM 64 basal medium supplemented with 2 mg L^{-1} of 2,4-D, callus was not produced. However, 2.0% of Chinese Spring anthers formed calli on N_6 medium supplemented with 100 mg L^{-1} glutamine, 100 mg L^{-1} of serine, 500 mg L^{-1} inositol, and 2 mg L^{-1} of 2,4-D (Shimada, 1981).

The use of natural extracts such as potato in media is advantageous because of ease in preparation and low cost. Their disadvantage is the unknown substances (and their unknown concentration) in the extracts. With synthetic or chemically defined media, individual components or groups of components can be adjusted stepwise to measure their effect on callus induction and plantlet regeneration.

Media used for regeneration of plantlets from microspore calli usually have the same composition as the callus-inducing media, except for the hormonal components. The growth hormones are either omitted or their composition changed.

7F-1.1.3.3 Effect of Culture Environment. Temperature is an important factor in callus induction and different genotypes exhibit different optimal temperature requirements. Ouyang et al. (1983) classified several cultivars, F_1 hybrids, anther culture-derived pollen lines, and *Agropyron elongatum* addition and substitution lines into high temperature (33 °C), low temperature (26 °C), and intermediate or insensitive types. In temperature trials, they found that all genotypes produced more calli and higher regeneration frequencies at 26 than at 22.5 °C. In the temperature range from 25 to 30 °C, the freqency of callus induction increased directly with temperatures for most genotypes. High temperature treatment did not decrease regeneration of high temperature types. However, for low temperature type cultivars, green plantlets were obtained only at 26 °C. For some genotypes, albino plantlets tended to increase with an increase of culture temperature from 26 to 32 °C. Also, somatic cells from anther filaments tended to form calli at high temperatures. It appears that the optimal culture temperature for most wheat genotypes lies between 26 and 30 °C.

Light is not essential for growth initiation. In fact, keeping the inoculated anthers in darkness appears to be necessary for callus formation. However, light for 10 to 14 h per day may be beneficial for post-initiation growth. Effect of light quality (wavelength) on callus growth and regeneration in wheat is unknown. Most researchers use cool white inflorescent bulbs at an intensity of around 1 to 2μE m^{-2} s^{-1}.

Humidity is not a factor, being at nearly 100% in the sealed containers in which the cultures are grown.

7F-1.1.3.4 Effect of Auxins and Cytokinins. The endogenous levels of these hormones in wheat microspores appear to be different in different cultivars, and exogenous hormones are required to trigger the growth of microspores. Although plants are autotrophic for auxins, specific concentrations of auxins and cytokinins are normally included in the culture medium to initiate the growth of wheat microspores while keeping the somatic tissues quiescent. A deviation from the optimum levels of hormones may induce callus formation from the somatic cells while keeping the haploid microspores quiescent. The most commonly used hormones are 2,4-D (2 to 4 mg L^{-1}) and kinetin (1 to 2 mg L^{-1}) for callus induction; indole-3-acetic acid (IAA) $C_{10}H_9NO_2$) (1 mg L^{-1}) or α-naphthaleneacetic acid (NAA) and kinetin (2 mg L^{-1}) for regeneration.

7F-1.1.4 Genetic Control of Callus Formation

Genotypes differ greatly in the frequency of callus induction on the same medium and it is reasonable to assume that callus formation is under genetic control. Anthers from Chinese Spring ditelosomic-4A and nullsomic-4A plants produced significantly more calli than those from the normal disomic, ditelos 1AL, 2AS, 3Aα, 5AL, 6Aα, 7AS, nulli-1A, nulli-2A, and mono-4A, indicating that some genetic factors inhibiting

callus formation are located on chromosome arm 4A (Shimada and Makino, 1975). However, calli induced from these two strains originated from anther filaments and were diploid. Whether or not the induction of pollen calli is under the same control system remains to be investigated.

7F-1.1.5 Morphological and Cytological Variability

Up to 100% of regenerated plantlets may be albinos (Ouyang et al., 1983). The exact cause of albinism is uncertain but calli cultured under high temperatures (30 to 32 °C) tend to produce more albinos than those cultured under low temperatures. Gene mutation was not the major cause of albinism (He and Ouyang, 1982), and microspores containing micronuclei usually led to the formation of albino regenereants (Chu et al., 1978). Morphological variations observed among R_1 (first generation regenerated) plants included short culm, curved rachis, seeds lacking endosperm, etc. Regenerated plantlets may vary from 1x to 6x, and may be mixoploid or nulli-haploid (lacking one chromosome).

Fertility of the R_1 plants varies and is mainly related to ploidy levels. Among 1630 plants examined, the proportions of sterile, fertile, and partially fertile plants were 73.1, 22.8, and 4.1%, respectively (Hu et al., 1978). Chromosome counts of randomly selected R_1 plants showed that 35.3% were haploid, 53.4% were diploid, and 11% were polyploid and mixoploid. Regenerated plantlets varied greatly in chromosome numbers ($2n=12$ to $2n=42$) and a low frequency (60%) showed the expected chromosome number ($2n=42$). The polyploid frequency increases directly with length of time on the induction medium. Nuclear fusion, endomitosis, and restitution nuclei all may contribute to the occurrence of polyploids obtained in anther culture.

7F-1.1.6 Pollen Calli

Pollen or microspore calli may be obtained by mechanical disruption of anthers, followed by centrifugation and resuspension into media. Alternatively, anthers can be floated on shallow layers of a liquid medium into which pollen will be shed. The floating anther technique is simple, free from maternal anther tissue, and applicable to large-scale manipulations (Sunderland and Roberts, 1977).

To initiate pollen growth, N_6 medium supplemented with 800 mg L^{-1} supplemented with 250 mg L^{-1} lactalbumin hydrolysate and 0.5 mg L^{-1} kinetin, and then incubated at 26 °C with 10-h illumination at an intensity of 2-k lux ($\sim 65\mu E\ m^{-3}\ s^{-1}$) 1982). Calli (diameter 1 to 3 mm) are transferred to an agar medium containing MS basal medium plus 0.3 mg L^{-1} IAA and 1.0 mg L^{-1} kinetin ($C_{10}H_9N_5O$). Calli with green shoots developing are transferred to a medium containing half strength MS basal components plus 2% sucrose, 0.5 mg L^{-1} IAA 0.1 mg L^{-1} kinetin for development of a root system.

This pollen culture technique produces calli at a much higher rate than culture on an agar medium using the same genotypes, but the fre-

quency of green plantlet regeneration is much lower than in anther culture. Transfer of the young pollen embryos or induced anthers from the liquid medium to an agar medium for 14 days, then transfer back to the liquid medium may increase the frequency of regenerated green plantlets (Henry and De Buyser, 1981).

7F–1.2 Wide Crosses

When *Hordeum vulgare* ($2n=2x=14$) is crossed to *H. bulbosum* ($2n=2x=14$ and $2n=4x=28$), a high frequency of haploids is obtained as a result of fertilization and subsequent elimination of the *H. bulbosum* genomes in the developing embryos (Kasha, 1974; Islam and Shepherd, 1981). When Chinese Spring wheat was crossed to $2x$ and $4x$ *H. bulbosum*, Barclay (1975) obtained 13.7 and 43.2% seed set, respectively. However, Zenkteller and Straub (1979) obtained only 2.18% seed set when Chinese Spring was crossed to $2x$ *H. bulbosum*, and Pental and Gunckel (1980) obtained only 0.2% of haploid plantlets from the same cross.

Chinese Spring and some Australian wheats, such as 'Gamut,' 'Timgalen,' 'Songlen,' and 'Wren' are crossable with *H. bulbosum*. Many European and U.S. wheat cultivars, however, cannot be crossed with *H. bulbosum* because embryo and endosperm fail to develop (Zenkteller and Straub, 1979). By chromosome substitution (Hope/Chinese Spring), it was found that chromosomes 5A and 5B, which carry the Kr_2 and Kr_1 loci, respectively, significantly reduced the crossability to *H. bulbosum*. Chromosome 5D also had an effect, but it was not as potent as that of chromosomes 5A and 5B (Snape et al., 1979).

Crosses between wheat and several other *Hordeum* spp. produced either no haploids or a frequency too low for practical use.

7F–1.3 Alien Cytoplasms

The ability of the cytoplasm from *Aegilops caudatum* (C cytoplasm) to induce haploids in wheat was discovered by Kihara and Tsunewaki (1962). When the nucleus of wheat strain 'Salmon' was introduced to *Ae. caudatum* cytoplasm by repeated backcrosses, approximately 30% haploid and 11% twin seedlings appeared in the offspring. Salmon, a common wheat derived from a cross between two 8x triticales, possessed a wheat-rye chromosome translocation (1B/1R), a modified chromosome 2B, and normal wheat cytoplasm.

When cytoplasms of different species in the genera *Aegilops* and *Triticum* were tested in the presence of the Salmon nucleus, C, C^u, M^u, Mt, and S^v induced haploids at various rates and A, D, G, M, M^h, M^o, S, and S^l were non-inducing. All the haploid-inducing species had genome C^u in common (Tsunewaki et al., 1974; Tsunewaki et al., 1976).

The frequency of haploids varied with the type of cytoplasm and the pollen parent (Mukai, 1981). For example, (kotschyi)-Salmon (*A. kotschyi* cytoplasm with the Salmon nucleus) produced haploids at a relatively

high frequency, but (kotschyi)-Chinese Spring and (kotschyi)-Spelta did not produce haploids. Failure to induce haploids by the latter suggests that the cytoplasmic genes in *A. kotschyi* interact with appropriate nuclear genes to produce haploids. In other words, a gene or genes in the rye chromosome 1R appeared to be responsible for the production of haploids when in combination with certain cytoplasms (Kobayashi and Tsunewaki, 1980).

7F–1.4 Gynogenesis

Female gametophytes of angiosperms can be induced to develop sporophytically. Usually the pistil, either with or without stamens, is cultured on the nutrient medium, but flower buds, whole flowers, ovaries, ovules, or portions of the inflorescence can also be cultured. To induce calli, the basic medium for culturing unpollinated ovaries or ovules in wheat is N_6 plus 2,4-D (2 mg L^{-1}) and sucrose (8%). The stage of inoculation appears to be from the uninucleate to mature stage. As in anther culture, genotypic response differs in ovary and ovule culture. The percentage of ovaries producing gynogenic calli in four wheat cultivars has been reported to vary from 1.3 to 10.9% (Zhu et al., 1981; Yang and Zhou, 1982).

A problem associated with ovary and ovule culture is the proliferation of somatic tissues that results in callus or embryoid formation. Formation of callus from somatic tissues may introduce substances inhibiting callus formation or growth from egg cells and make the identification of haploid calli difficult. Hormonal balance may play a role in inducing gynogenesis without triggering the proliferation of somatic tissue.

Under certain conditions, ovary or ovule culture can produce exclusively haploid plantlets. In other cases, plants of different ploidy levels can be produced. Polyploids may originate from a spontaneous doubling of chromosomes during callus proliferation rather than from somatic tissues. Both green and albino plantlets have been regenerated from ovary-derived calli.

Gynogenesis can be used as a supplement to other approaches for haploid production. For example, when haploids are desired from male sterile plants, gynogenesis offers a useful tool for obtaining them. Also, in vitro culture of immature ovaries, pistils, and ovules provides a basis for further study of megasporogenesis and the transformation of female gametophytic cells into sporophytic cells in the absence of fertilization. Much remains to be done before this procedure can become a practical and useful technique in wheat improvement.

7F–1.5 Applications

Wheat haploids are of theoretical and applied interest. Induced haploid sporophytes may play a key role, not only in increasing the efficiency of breeding programs by producing pure lines rapidly, but also in the elucidation of fundamental genetics.

The potential for using homozygous lines directly in plant breeding has been recognized for a long time. The rapid production of homozygotes from heterozygotes is obviously an advantage of the haploid breeding programs over the traditional selfing methods. A second advantage of the haploid approach could be the increased selection efficiency. For example, if there are n independent loci controlling a trait, then using anther culture a minimum of 2^n plants is required to represent all homozygous genotypes, whereas using traditional breeding methods 4^n plants are needed (Clapham, 1977). Another advantage of the anther culture techniques is the flexibility of using F_1, F_2, or backcross plants.

In mutation research, haploid plantlets, calli, or cells have an advantage over their diploid counterparts since recessive mutants are expressed. In addition, haploid wheat plantlets also may be used to elucidate host-parasite relationships, to obtain spontaneously occurring aneuploids, to analyze chromosome behavior, and to study mini-microspores (microspores containing 1 to 5 chromosomes) for their possible use in transferring a few chromosomes from donor plants to the recipient cells (Hao et al., 1980).

7F–1.6 Limitations and Perspectives

Considerable progress is being made with wheat anther culture. The most desirable age for microspores at inoculation has been defined, the need for low temperature pretreatment of anthers or spikes has been determined, the culture environment has been explored, both potato and chemical media have been formulated, and regeneration of callus is fairly successful. The dihaploids derived from regenerated plantlets are usually homozygous, fertile, and equal in vigor to normal wheat plants.

However, important problems remain to be solved. Microspores must pass through a callus phase from which plantlets are later regenerated. This two-step procedure may result in changes in chromosome structure and number and a high frequency of albinos among regenerated plantlets. Frequency of regeneration is still low and of doubtful practical significance, and the regenerated plantlets may not represent the complete gametic array produced by the F_1 hybrids. Doubling of chromosome number by the colchicine-DMSO mixture is not 100% effective. The preservation of spikes and anthers to provide a constant supply of material has not been investigated.

It is evident that success in producing haploids at high frequencies requires a long-term, cooperative plan, taking into account all the factors that influence callus formation and plantlet regeneration.

7F–2 SOMATIC TISSUE CULTURE

Somatic tissue culture is a necessary step in the exploitation of many of the new technologies for wheat improvement. Somatic hybridization

via protoplast fusion, chromosome transplants, and DNA injections to the nucleus are emerging techniques requiring an in vitro stage for cells of the target crop. Recombinant DNA typically makes use of host-species' cells in vitro for gene vectors, but methods are being developed to eliminate this phase and have gene vectors transform cells in vivo. The reason for this is a problem common to each of the above mentioned techniques: in order to develop a genetically superior wheat crop, whole, fertile plants must be obtained from the cells transformed in vitro. Single somatic cells or protoplasts from wheat have not been reported to regenerate into plants. The control of regeneration of wheat plants from single cells in vitro must be elucidated before somatic hybridization, chromosome transplant, DNA injection, and perhaps recombinant DNA technology can be routine tools in wheat breeding.

7F–2.1 Somaclonal Variation

Wheat plants can be regenerated from groups of cells. Although the frequency of regeneration is not as high as for some other types of plants, notably members of the Solanaceae, it is high enough to make the application of somaclonal variation to wheat improvement feasible.

Somaclonal variation is the term given to the spontaneous genetic alteration occurring in cells growing in vitro (Larkin and Scowcroft, 1981). It has long been known that spontaneous genetic aberrations do occur in cultured cells, with gross chromosomal changes (aneuploidy, polyploidy, etc.) frequently observed (Bennici and D'Amato, 1978). More recently, subtle genetic changes in cultured cells have been reported. These are the basis for hope that crop species can be improved in subtle ways through tissue culture without interfering with a large portion of the genome and without introducing alien or exogenous genetic material.

The mechanism of action of somaclonal variation is not understood, but enough evidence is available to show that it is not an artifact. When several regenerants are produced from one source tissue (therefore one genotype) and the regenerants and their progeny differ from the parent, that is good evidence that genetic variation has taken place, even in the absence of known mutagens.

Two factors seem important in somaclonal variation. First, cultured cells should pass through a disorganized growth phase, such as in a callus or suspension culture, in order to observe variation in the subsequent regenerants. Regenerants produced from embryo or shoot meristem culture that continue their normal developmental pathway (i.e., the elaboration of a plantlet or shoot) rarely exhibit somaclonal variation. This is important to those interested in cloning desirable genotypes without introducing variation. The second, related point is that the frequency and degree of variation exhibited by regenerated plants is proportional to the time spent in the disorganized growth phase. Work from several labs illustrates this point, but the report by McCoy et al. (1982) is exemplary. They cultured tissue from two cultivars of oats and found that there was

a steady increase in chromosomal aberrations over time for both cultivars, but that one was more prone to mutation than the other. This might explain why different species or culture conditions can lead to differences in the degree of variation observed, and also why the regeneration capability diminishes over time—a build up of minor mutations or the increased chance of mutating a critical gene could result in nonreorganization, and, therefore, no regeneration would occur from the affected cells.

Single genes can be affected by somaclonal variation as well as the chromosomal changes. Evans and Sharp (1983) obtained several single gene mutants in tomato (*Lycopersicon esculentum* Mill.) plants derived from tissue culture and are selecting improved genotypes from the variant tomatoes. Variants are also being observed in wheat regenerants in several laboratories around the world, but the genetic documentation for these is not as clear as for tomato and some other species, presumably because of the relatively late elucidation of the regeneration processes for wheat cells in vitro.

7F–2.2 Procedures

There are two popular methods for producing somaclonal variants in wheat. One involves the culture of the immature embryo and the subsequent regeneration via somatic embryogenesis from the scutellar tissue; the other involves the induction of shoots from callus tissue derived from the leaf base or young seedling. The general procedure for immature embryo culture involves collecting caryopses 14 to 16 days after fertilization, then excising the embryo and placing it, scutellum up, on the surface of the initial culture medium. Embryos younger than about 14 days after fertilization do not respond as well to the culture conditions, while those over 16 days tend to germinate normally. Regenerants from callus from embryos older than 16 days have been reported, but the frequency tends to be lower. Media will vary according to genotype and researcher. One common medium is that used by Sears and Deckard (1982), a Murashige and Skoog (1962) basal medium, with 150 mg L^{-1} asparagine, 0.5 mg L^{-1} thiamine HCl, 1 mg L^{-1} 2,4-D, and 2% sucrose added. Cultures usually are maintained under natural conditions (i.e., at room temperature, with light and dark periods), and are transferred to fresh media every 4 to 6 weeks. Shoot regeneration is induced upon transfer of regenerable callus to a regeneration medium such as that used by Ahloowalia (1982), a half-strength MS basal medium with lower auxin levels, or that of Sears and Deckard (1982), a basal medium with the 2,4-D level reduced to 0.1 mg L^{-1}. Other scientists find that regeneration occurs spontaneously and does not require a transfer of tissue to a medium of different composition (e.g., Maddock et al., 1983; Ozias-Akins and Vasil, 1982; Eapen and Rao, 1984). In most of these cases of regeneration from the scutellar callus, the young shoot is transferred ultimately to a medium devoid of hormones to permit the establishment of plantlets with roots.

Regeneration from callus via shoot organogenesis has also been used successfully. Young leaves most readily form callus on MS basal medium (Ahuja et al., 1982) or on MS or Norstogs B_{11} (Norstog 1973) basal medium (McHughen, 1983), in each case supplemented with from 0.2 to 4 mg L^{-1} 2,4-D. Shoot formation occurs on transfer of this callus to MS medium with 0.05 mg L^{-1} NAA and 0.5 mg L^{-1} benzylaminopurine (BAP) (Ahuja et al., 1982) or MS medium with 1 mg L^{-1} each of IAA and kinetin added (McHughen, 1983). Callus induction and subsequent regeneration of plants seems to be highly genotype-dependent. A culture system (chemical plus physical environment) might be highly efficient for one cultivar, but another cultivar might not respond at all. For example, Nabors et al. (1983) reported that a medium containing 5 mg L^{-1} 2,4,5-T, 20 mg L^{-1} tryptophan and 0.5 mg L^{-1} kinetin produced the most embryogenic callus from the hard red spring wheat 'Chris'. When the procedure was tried using hard red spring wheats 'Neepawa' and 'Columbus', the tissues promptly died (McHughen, unpublished). Both of the cultivars do respond and produce regenerants under other culture conditions (Orshinsky and McHughen, 1984).

A wide range of media are suitable for evoking callus formation and subsequent regeneration of plants, and most, if not all, cultivars have been successfully regenerated from cells in vitro, even if at a low efficiency. Not all cultivars respond to all of the reported induction or regeneration media, nor do closely related cultivars necessarily respond similarly to a given medium. A judicious approach to regenerating plants from a cultivar not previously reported to have been regenerated would be to mimic the procedure successful for a closely related cultivar, observe the efficiency, then begin modifying the culture conditions to increase the efficiency for the new cultivar.

Alternatively, one could try breeding for culture response in a new cultivar. Culturability and regenerability seem to be under fairly simple genetic control in wheat (Salman et al., 1984). One could cross a highly regenerable cultivar with the nontested or low regenerable-efficiency cultivar and select for culturability from the progeny. This method would have the disadvantage of requiring backcrossing to reduce the undesired genetic components from the culture-efficient parent. In general, it would probably be easier to alter the culture conditions to improve regenerability in a novel cultivar than to breed for it, especially if the novel cultivar is already a highly adapted, premium-quality line.

Regeneration of wheat using both methods (somatic embryogenesis from scutellar callus and shoot organogenesis from leaf or other callus) is being used to produce somaclonal variants. Regeneration from immature embryo callus is more efficient than from leaf callus, but, if it is true that regenerants from organized tissue or from tissue passing through a short callus phase will have fewer variations, regenerants from leaf base callus may have a higher frequency of variants. Therefore, if the objective is to derive variants for crop improvement, the leaf base callus system

might be more efficient, in spite of producing a lower frequency of regenerated plants. In fact, Vasil (1983) claims no variants were observed in somatic embryogenic regenerants of wheat. A comparison of the two methods for such efficiency is currently being investigated in at least two laboratories.

7F–2.3 Origin and Value of Variants

The spectrum of variants observed is broad. Some variants are similar to what might be expected from mutation treatment, but evidence is mounting that somaclonal variation does not follow the same pattern as induced mutation (Evans et al., 1984). Instead of destroying parts of the genome, as is common in induced mutations, somaclonal variants seem to arise from a relaxed control of the genome by the cell. Transposable elements have been implicated in explaining somaclonal variation, due essentially to the sometimes unusual nature of the variant trait or its stability. Genetic instability of variant traits is not unusual and could be explained by a transposable element, as has recently been hypothesized in alfalfa (*Medicago sativa* L.) (Groose and Bingham, 1984), triticale (Jordan, 1984), and wheat (Larkin et al., 1984; Woloschuk and McHughen, 1984). So far no direct evidence of a transposable element has been provided. Transposable elements are not likely to be the exclusive agent of somaclonal variation in any case, as they would not be responsible for the gross chromosomal aberrations associated with prolonged culture.

Whatever the cause, tissue culture has produced variants in many crops, including wheat. As with induced mutations, most of the variants have no agronomic value, but some do. Some of the variant traits observed in wheat, such as white grain color in a 'Yaqui 50E' variant (Larkin and Scowcroft, 1981), are simply inherited. Other variant traits are more complex and affect quantitative characters such as days to maturity and 1000 kernel weight (Larkin et al., 1984; Woloschuk and McHughen, 1984), while others do not seem to follow the usual rules of genetics, such as homozygous mutant genes (variants that appear in the regenerated plant and do not segregate in subsequent generations) (Larkin et al., 1984). A selection of variants observed in wheat regenerants or their progeny is given in Table 6F–2.

7F–2.4 The Value of the Somaclonal Variation Procedure

The advantage of using somaclonal variation in wheat (or any crop) breeding is that it exploits the genetic potential that already exists in a desirable background. By using a well adapted cultivar in a somaclonal variation program, a breeder can select for additional desired traits, such as salt tolerance or herbicide resistance, at the cellular level, or select among the progeny of regenerants either for an expected desired type (e.g., higher yield, earlier maturity) or for characters previously unknown,

Table 7F-2. Sample of variants observed in regenerants of wheat (*Triticum aestivum* L.) or their progeny.

Variant trait†	Genotype	Source tissue	Level of selection	Stability‡	Reference
None	N/A	Immature embryo	Plant	Y	Vasil, 1983
Albino	Flanders	Immature embryo	Plant	?	Maddock et al., 1983
	CI–13198	Immature embryo	Plant	?	Sears and Deckard, 1982
	NI–4; Hira	Mature embryo	Plant	?	Eapen and Rao, 1982
	Siete Cerros	Immature embryo	Plant	?	Ahloowalia, 1982
Height	Highbury	Immature embryo	Plant	?	Maddock et al., 1983
	Maris Huntsman	Immature embryo	Plant	?	Ahloowalia, 1982
	NI–4	Embryos	Plant	Y	Eapen and Rao, 1984
	Yaqui 50E	Immature embryos	Plant	Y	Larkin et al., 1984
	Neepawa; Columbus	Callus	Plant	Y	McHughen, unpublished§
Salt-tolerance	Chris	Mature embryos	Cell	?	Heyser et al., 1985
	Neepawa; Columbus	Callus	Cell	?	McHughen, unpublished§
Leaf or stem morphology	Maris Huntsman	Immature embryos	Plant	?	Ahloowalia, 1982
	Yaqui 50E	Immature embryos	Plant	Y	Larkin et al., 1984
	Neepawa; Columbus	Callus	Plant	N	Woloschuk and McHughen, 1984

(continued on next page)

Table 7F-2. (Continued)

Variant trait†	Genotype	Source tissue	Level of selection	Stability‡	Reference
Spike or kernel morphology	Maris Huntsman	Immature embryos	Plant	?	Ahloowalia, 1982
	Highbury	Immature embryos	Plant	?	Maddock et al., 1983
	Yaqui 50E	Immature embryos	Plant	Y	Larkin et al., 1984
	Neepawa; Columbus	Callus	Plant	Y	McHughen, unpublished§
	(winter wheat)	Immature embryos	Plant	?	Johnson and Nguyen, 1984
1000 kernel wt., total wt/plant	NI–4	Embryos	Plant	Y	Eapen and Rao, 1984
	Neepawa; Columbus	Callus	Plant	Y	McHughen, unpublished§
Time to flowering, maturity	Highbury	Immature embryos	Plant	?	Maddock et al., 1983
	Yaqui 50E	Immature embryos	Plant	Y	Larkin et al., 1984
	Columbus	Callus	Plant	Y	McHughen, unpublished§
	(winter wheat)	Immature embryos	Plant	?	Johnson and Nguyen, 1984
Waxiness, gliadin band patterns, hormonal responses	Yaqui 50E	Immature embryos	Plant	Y	Larkin et al., 1984

†Few of these variants are genetically characterized yet, but, genetically stable or not, they indicate the type of changes that can be produced. Presumably, any unstable genetic trait can exist in a stable form, so this table includes those variants that have not been proved stable. Stability is determined by whether the variant trait was observed to have been passed through at least one seed generation.
‡Y = Yes, ? = not reported or not tested.
§Data available from McHughen upon request.

such as double-leaved (two leaves per node) wheat (McHughen, unpublished).

A disadvantage of using somaclonal variation is that variant traits are often unstable, so any variant must be carefully observed for several generations to ensure stability, and also to ensure that, while gaining a desirable novel trait, the genome did not lose some other critical trait such as a disease resistance.

Somaclonal variation is a feasible method for application in wheat breeding programs. Its main advantage may be the ability to add to good cultivars one or two traits not otherwise readily obtainable. Somaclonal variation is not likely to turn a poorly adapted, low quality wheat into a superb cultivar. While there is no longer debate on the reality of somaclonal variation, the technique will prove valuable to wheat breeding even if genetic changes do not occur in cells in culture. Because of the inherent genetic variation in a population of wheat, and because every wheat regenerant (and its progeny) is so carefully scrutinized by the scientist employing somaclonal variation, superior strains will be selected without necessarily having undergone genetic alterations in vitro. That is, superior strains are already present within a given genotype, but these tend to go unnoticed in the field. If a plant from such a strain happens to undergo culture and regeneration, its superior traits will be observed even if genetic changes do not occur in vitro.

7F–3 DINITROGEN FIXATION

7F–3.1 Dinitrogen-Fixing Bacterial Species

Intensive agriculture has led to a great emphasis on research on biological N_2 fixation, to conserve energy. The energy required to produce 1 ton of N fertilizer is estimated to be equivalent to seven barrels (1.11 h.L) of oil (Döbereiner, 1978). Atmospheric N_2 is fixed by bacteria containing the enzyme nitrogenase, which catalyzes the reduction of N_2 to NH_4^+. Some bacteria fix N_2 without aid; others require a symbiotic host, usually a eukaryotic species.

In addition to a symbiotic relationship between legumes and bacteria in N_2 fixation, there is also evidence that associations occur between N_2-fixing bacteria and nonlegume plants. Wheat cells cannot reduce N_2 directly to NH_4^+ because they lack the enzyme nitrogenase, but they may benefit from an association with certain N_2-fixing bacteria. The major bacteria known to associate with wheat are *Azospirilla*, *Rhizobium*, and *Bacillus* spp. (Larson and Neal, 1978). Three strains each of *Bacillus polymyxa* and *Enterobacter cloacae*, and one strain of *B. macerans* were isolated from wheat roots in Oregon (Nelson et al., 1976). Two species of the genus *Azospirilla*, *A. lipoferum*, and *A. brasilense*, have also been isolated. The two *Azospirilla* spp. make up 1 to 10% of the total bacterial population of the rhizosphere (Okon, 1982). *Azospirilla* spp. can carry

out most of the N-transforming reactions of soil N_2 fixation, assimilation of NH_4^+ and NO_3^-, mineralization of organic N, and denitrification. They are closely associated with the root systems, mainly embedded in the mucigel layer and between cortex cells. *Azospirilla* are adsorbed onto roots in significantly higher numbers than cells of other N_2 fixers. Plants associated with *Azospirilla* produce more root hairs and lateral roots than do uninfected ones.

Rhizobium spp. are the major group of bacteria having a symbiotic relationship with legumes. Some *Rhizobium* strains such as the cowpea strain 32H1 and *R. japonicum* also are associated with grasses such as wheat.

7F–3.2 Factors Affecting Dinitrogen Fixation

Many factors involved in nitrogenase activity in the rhizosphere of grasses affect N_2 fixation. These factors include genotype, plant age, light intensity, air temperature, water deficit, soil temperature, soil inorganic N content, and the nature and number of N_2 fixers (diazotrophs) associated with grass roots (Balandreau et al., 1978). They may act at different levels through photosynthesis, translocation, and exudation, or directly on the N_2-fixing bacteria.

Plant genotypes may be crucial in determining whether an association occurs between the host and the N_2-fixing bacteria. A host genotype that fosters such associations should be able to excrete C compounds to supply energy for the bacteria. When *Triticum aestivum* 'Cadet' and its substitution lines carrying individual 'Rescue' chromosomes were inoculated with either *Bacillus* C-11-25 or *A. brasilense* (ATCC29145) in nutrient solution in a phytotron, an increase in plant dry matter and total N was noted in all lines except C-R5B (Cadet with chromosome 5B from Rescue). On the other hand, Rescue lines with chromosomes substituted from Cadet were unaffected by inoculation, except for R-C5B and R-C5D (Rennie and Larson, 1979).

Different types of N_2-fixing bacteria differ in the effectiveness of their association with the roots of wheat. A tight control of the nitrogenase synthesis could allow the bacteria to fix sufficient N_2 for their own use but none for the host plant. In addition, natural N_2-fixing associations could have an activity too low to contribute a significant N input to the plant (Brill, 1980).

Some results suggest that the associations may result in variable increases in N content and vegetative growth, and the variation may be caused by release of plant growth hormones or by enhanced mineral uptake.

The stable N_2-fixing association established in the laboratory may not be maintained under field conditions. Competition with other bacteria for excreted plant C and for attachment sites on the roots could be major barriers. Usually the strains which have been inoculated first and at a high concentration have an advantage (Hess et al., 1983).

7F–3.3 Effect of Inoculation

It has been reported that inoculation of field-grown wheat with N_2-fixing rhizosphere *Azospirillum* bacteria benefits plant growth, dry weight, total N content, and grain yield (Kapulnik et al., 1983).

Isolates of *A. lipoferum* and *A. brasilense* usually vary in their denitrifying and N_2-fixing capacity. A strain of *A. lipoferum* with high N_2-fixing ability and a negative test for denitrification was isolated from the rhizosphere of wheat plants. Inoculation of wheat seeds with this strain stimulated grain and straw production (Table 7F–3) (Rai and Gaur, 1983).

When *T. turgidum* 'Inbar' was inoculated with two strains of *A. brasilense* under field conditions, grain yield was increased by 5.2 and 10.9%, respectively (Kapulnik et al., 1983). However, seed protein was not affected by inoculation. When *T. aestivum* 'Barkai' was inoculated with a mixture of the two strains, increases occurred in grain yield (7.9%), shoot weight (17.9%), number of tillers, and plant height. Inoculation also increased plant N percentage and N yield per ha. These results suggest that inoculation increased the availability of N to the plants.

The mechanisms by which an association with diazotrophic bacteria benefits wheat under field conditions are not clearly understood. Nevertheless, the *Azospirillum*–root association has marked effects on root branching, root development, and the root's reaction to inoculation, by producing growth-promoting factors (Kapulnik et al., 1983).

Whether or not inoculation will increase wheat yields consistently in the field remains to be assessed. While inoculation has provided some positive effects on wheat production, it is necessary to determine to what extent inoculation affects each of the developmental phases of the plant and how environmental fluctuations, such as water deficit and high temperature stress, affect the results of inoculation. Other ecological factors also may either accelerate or inhibit the N transfer process in the bacteria–wheat associative fixation system. There are many problems that need to be answered before inoculation of wheat with N_2-fixing bacteria can have a practical and beneficial use.

Table 7F–3. Grain and straw yield (kg ha^{-1}) of wheat inoculated with a strain of *A. lipoferum* at three levels of N†.

Treatment	Grain yield	Straw yield
Control	1260	1788
Inoculation	2070	2110
40 kg N	2370	3240
40 kg N + inoculation	3110	3820
80 kg N	2960	3690
80 kg N + inoculation	4150	4890
Std error	230	220

†Fertilization of other elements: P_2O_5, 60 kg ha^{-1}; K_2O, 40 kg ha^{-1}.

REFERENCES

Aase, H.C. 1930. Cytology of *Triticum*, *Secale*, and *Aegilops* hybrids with reference to phylogeny. Wash. State Coll. Bull. 2:5–60.

———. 1946. Cytology of cereals. II. Bot. Rev. 12:255–334.

Adams, M.W. 1982. Plant architecture and yield breeding. Iowa State J. Res. 56:225–254.

Ahloowalia, B.S. 1982. Plant regeneration from callus cultures in wheat. Crop Sci. 22:405–410.

Ahuja, P.S., D. Pental, and E.C. Cocking. 1982. Plant regeneration from leaf base callus and cell suspensions of *Triticum aestivum*. Z. Pflanzenzuecht. 89:139–144.

Allan, R.E. 1973. Yield of wheat hybrids of the *T. timopheevi* nucleocytoplasm system. p. 311–317. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August.

———. 1980. Influence of semidwarfism and genetic background on stand establishment of wheat. Crop Sci. 20:634–638.

———. 1983. Harvest indexes of backcross-derived wheat lines differing in culm height. Crop Sci. 23:1029–1032.

Allard, R.W., and R.G. Shands. 1954. Inheritance of resistance to stem rust and powdery mildew in cytologically stable spring wheats derived from *Triticum timopheevii*. Phytopathology 44:266–274.

Altman, D.W., and R.H. Busch. 1984. Random intermating before selection in spring wheat. Crop Sci. 24:1085–1089.

Amano, E. 1972. Genetic fine structure analysis of mutants induced by ethyl methanesulfonate. p. 43–59. *In* Chemical mutagenesis in microorganisms, and plants. 11th Gamma Field Symposium, Inst. Radiation Breeding, Ohmiya. Ibaraki, Japan. 25–26 July.

Anonymous. 1972. Genetic vulnerability of major crops. Nat. Acad. Sci., Washington, DC.

———. 1978. Conservation of germplasm resources, an imperative. Nat. Acad. Sci., Washington, DC. 1978.

Armstrong, J.M. 1936. Hybridization of *Triticuum* and *Agropyron*. I. Crossing results and description of the first generation hybrids. Can. J. Res. Sec. C 14:190–202.

———. 1945. Investigation in *Triticum–Agropyron* hybridization. Emp. J. Exp. Agric. 13:41–53.

———, and H.A. McLennan. 1944. Amphidiploidy in *Triticum–Agropyron* hybrids. Sci. Agric. 24:285.

Atashi-Rang, G., and K.A. Lucken. 1978. Variation, combining ability, and interrelationships of anther length, anther extrusion, glume tenacity and shattering in spring wheat. Crop Sci. 18:267–272.

Auerbach, C. 1976. Mutation research. Problems, results and perspectives. Chapman and Hall, London.

Austin, R.B., M.A. Ford, J.A. Edrich, and B.E. Hooper. 1976. Some effects of leaf posture on photosynthesis and yield of wheat. Ann. Appl. Biol. 83:425–446.

Avery, D.P., H.W. Ohm, F.L. Paterson, and W.E. Nyquist. 1982. Three cycles of simple recurrent selection for early heading in winter wheat. Crop Sci. 22:908–912.

Backhouse, W.O. 1916. Note on the inheritance of "crossability." J. Genet. 6:91–94.

Bailey, J.B., Jr., and R.E. Comstock. 1976. Linkage and the synthesis of better genotypes in self-fertilizing species. Crop Sci. 16:363–370.

Baker, R.J. 1969. Genotype-environment interactions in yield of wheat. Can. J. Plant Sci. 49:743–751.

———. 1971. Effects of stem rust and leaf rust of wheat on genotype-environment interaction for yield. Can. J. Plant Sci. 51:457–461.

Balandreau, J., P. Ducerf, I. Hamad-Fares, P. Weinhard, F. Rinaudo, C. Miller, and Y. Dommergues. 1978. Limiting factors in grass nitrogen fixation. p. 275–302. *In* J. Dob-

ereiner, et al. (ed.) Limitations and potentials for biological nitrogen fixation in the tropics. Plenum Press, New York.

Barbar, H.N., and A.G. Netting. 1968. Chemical genetics of β-diketone formation in wheat. Phytochemistry 7:2089–2093.

Barclay, I.R. 1975. High frequencies of haploid production in wheat (*Triticum aestivum*) by chromosome elimination. Nature (London) 256:410–411.

Bennici, A., and F. D'Amato. 1978. *In vitro* regeneration of durum wheat plants. I. Chromosome numbers of regenerated plantlets. Z. Pflanzenzuecht. 81:305–311.

Bhagwat, S.K., C.R. Bhatia, T. Gopalakrishna, D.C. Joshua, R.K. Mitra, P. Narahari, S.E. Pawar, and R.G. Thakare. 1979. Increasing protein production in cereals and grain legumes. p. 225–236. *In* Seed protein improvement in cereals and grain legumes. Vol. II. Proc. Int. Symp. on Seed Protein Improvement in Cereals and Grain Legumes. Neuherberg. 4–8 Sept. 1978. IAEA, Vienna. STI/PUB/496.

Borlaug, N.E. 1981. Preface. p. 1–2. *In* Indian multilines. CIMMYT. Mexico.

Bos, I. 1983. Some remarks on honeycomb selection. Euphytica 32:329–335.

Boyes, J.W., and W.P. Thompson. 1937. The development of endosperm and embryo in reciprocal interspecific crosses in cereals. J. Genet. 34:203–227.

Brennan, P.S., D.E. Byth, D.W. Drake, I.H. DeLacy, and D.G. Butler. 1981. Determination of the location and number of test environments for a wheat cultivar evaluation program. Aust. J. Agric. Res. 32: 189–201.

Brezhnev, D.D. 1977. The utilization of world plant gene pool of the U.S.S.R. in distant hybridization in plant breeding. p. 23–30. *In* E. Sanchez-Monge and F. Garcia-Olmedo, (ed.) Interspecific hybridization in plant breeding. Proc. 8th Cong. EUCARPIA. Madrid.

Brill, W.J. 1980. Nitrogen fixation. p. 53–76. *In* P.S. Carlson (ed.) The biology of crop productivity. Academic Press, New York.

Brock, R.D. 1977. When to use mutations in plant breeding. p. 213–219. *In* Manual on mutation breeding. 2nd ed. IAEA, Vienna. STI/DOC/10/119.

Browning, J.A., K.J. Frey, M.E. McDaniel, M.D. Simons, and I. Wahl. 1979. The biologic of using multilines to buffer pathogen populations and prevent disease loss. Indian J. Genet. Plant Breed. 39:3–9.

Brunori, A., H. Axmann, A. Figueroa, and A. Micke. 1980. Kinetics of nitrogen and dry matter accumulation in the developing seed of some varieties and mutant lines of *Triticum aestivum*. Z. Pflanzenzuecht. 84:201–218.

----, A. Figueroa, and A. Micke. 1984. Strategy of breeding for high grain protein content in *Triticum aestivum*. p. 321–332. *In* Cereal grain protein improvement. Proc. FAO/IAEA Res. Prog. for Cereal Grain Protein Improvement, Vienna, Austria. 6–10 Dec. 1982. IAEA, Vienna. STI/PUB/664.

Bullock, W.P., P.S. Baenziger, and G.W. Schaeffer. 1982. Anther culture of wheat (*Triticum aestivum* L.) F_1's and their reciprocal crosses. Theor. Appl. Genet. 62:155–159.

Busch, R.H., J.C Janke, and R.C. Frohberg. 1974. Evaluation of crosses among high and low yielding parents of spring wheat (*Triticum aestivum* L.) and bulk prediction of line performance. Crop Sci. 14:47–50.

----, and K. Kofoid. 1982. Recurrent selection for kernel weight in spring wheat. Crop Sci. 22:568–572.

Byrne, I., and D.C. Rasmusson. 1974. Recurrent selection for mineral content in wheat and barley. Euphytica 23:241–249.

Campbell, L.G., and H.N. Lafever. 1980. Effects of locations and years upon relative yields in the soft red winter wheat region. Crop Sci. 20:23–28.

Carvalho, F.I.F., and C.O. Qualset. 1978. Genetic variation for canopy architecture and its use in wheat breeding. Crop Sci. 18:561–567.

Chapman, V., and T.E. Miller. 1978. The amphiploid of *Hordeum chilense* × *Triticum aestivum*. Cereal Res. Commun. 6:351–352.

Chu, C.C., C.S. Sun, and C.C. Wang. 1978. Cytological studies on androgenesis of wheat (*Triticum aestivum* L.) p. 113–120. *In* H. Hu et al. (ed.) Proc. Symp. Anther Culture. Science Press, Peking.

Cisar, G., A.E. Howey, and C.M. Brown. 1982. Optimal population density and random vs. selective elimination of genotypes under a modified single-seed descent method with spring oats. Crop Sci. 22:576–579.

Clapham, D.H. 1977. Haploid induction in cereals p. 279–298. *In* J. Reinert and Y.P.S. Bajaj (ed.) Plant cell, tissue, and organ culture. Springer-Verlag New York, New York.

Conger, B.V. 1972. Control and modification of seed radio-sensitivity. Trans. Am. Soc. Agric. Eng. 15:780–784.

Cregan, P.B., and R.H. Busch. 1977. Early generation bulk hybrid yield testing of adapted hard red spring wheat crosses. Crop Sci. 17:887–891.

Dalrymple, D. 1978. Development and spread of high-yielding varieties of wheat and rice in the less developed nations. 6th ed. USDA Foreign Agric. Econ. Rep. 95. U.S. Government Printing Office, Washington, DC.

----. 1980. Development and spread of semi-dwarf varieties of wheat and rice in the United States. An international prespective. Agric. Econ. Rep. 455. USDA, Washington, DC.

de Kock, M. 1972. The actions of gamma irradiation and N-methyl-N nitrosourea in plants. Ph.D. diss. Washington State Univ.

Delibes, A., R. Sanchez-Monge, and F. Garcia-Olmedo. 1977. Biochemical and cytological studies of genetic transfer from the M^{v} genome of *Aegilops ventricosa* into hexaploid wheat: A progress report. p. 81–89. *In* E. Sanchez-Monge and F. Garcia-Olmedo (ed.) Interspecific hybridization in plant breeding. Proc. 8th Congr. Eucarpia, Madrid.

Deodikar, G.B., V.P. Patil, and V.S.P. Rao. 1979. Breeding of Indian *durum* and *dicoccum* wheats by interspecific hybridization with 4N *Triticum* species. Indian J. Genet. Plant Breed. 39:114–125.

DePauw, R.M., and L.H. Shebeski. 1973. An evaluation of an early generation yield testing procedure in *Triticum aestivum*. Can. J. Plant Sci. 53:465–470.

de Vries, A. Ph. 1971. Flowering biology of wheat, particularly in view of seed production—a review. Euphytica 20:152–170.

Dewey, D.R. 1983. Historical and current taxonomic perspectives of *Agropyron, Elymus* and related genera. Crop Sci. 23:637–642.

Döbereiner, J. 1978. Potential for nitrogen fixation in tropical legumes and grasses. p. 13–24. *In* J. Döbereiner et al. (ed.) Limitations and potentials for biological nitrogen fixation in the tropics. Plenum Press, New York.

Donald, C.M. 1962. In search of yield. J. Aust. Inst. Agric. Sci. 28:171–178.

----, 1968. The breeding of crop ideotypes. Euphytica 17:385–403.

----, and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agron. 28:361–405.

Donini, B., T. Kawai, and A. Micke. 1984. Spectrum of mutant characters utilized in developing improved cultivars. p. 7–31. *In* Selection in mutation breeding. Proc. of Consult. Meet., Vienna, Austria. 21–25 June 1982. IAEA, Vienna. STI/PUB/665.

Dosba, F., and Y. Cauderon. 1972. A new interspecific hybrid: *Triticum aestivum* ssp. *Vulgare* × *Aegilops ventricosa*. Wheat Inf. Serv. 35:22–24.

----, and G. Doussinault. 1977. Introduction into wheat of the resistance to eyespot in *Aegilops ventricosa*. p. 99–107. *In* E. Sanchez-Monge and F. Garcia-Olmedo (ed.) Interspecific hybrdization in plant breeding. Proc. 8th Cong. Eucarpia, Madrid.

Doussinault, G., A. Delibes, R. Sanchez-Monge, and F. Garcia-Olmedo. 1983. Transfer of a dominant gene for resistance to eyespot disease from a wild grass to hexaploid wheat. Nature (London) 303:698–700.

Driscoll, C.J. 1972. XYZ system of producing hybrid wheat. Crop Sci. 12:516–519.

----. 1978. Registration of 'Cornerstone' male sterile wheat germplasm. Crop Sci. 17:190.

----. 1981. New approaches to wheat breeding. p. 97–106. *In* L.T. Evans and W.J. Peacock (ed.) Wheat science today and tomorrow. Cambridge University Press, Cambridge.

----. 1984. Semi-dwarf mutants in Triticale and wheat breeding. p. 101–110. *In* Semi-dwarf cereal mutants and their use in cross-breeding Vol. II. Proc. Res. Coord. Meet. on Evaluation of Semi-Dwarf Cereal Mutants for Cross Breeding, Davis, CA. 30 Aug.–3 Sept. 1982. IAEA, Vienna. TECDOC-307.

----, and K.K. Barlow. 1976. Male sterility in plants: Induction, isolation and utilization. p. 123–131. *In* Induced mutations in cross-breeding. Proc. of an Advisory Group, Vienna, Austria, 13–17 Oct. 1975. IAEA, Vienna. STI/PUB/447.

Dunwell, J.M. 1978. Anther culture—Division and differention in cultured pollen. p. 103–112. *In* T.A. Thorpe (ed.) Frontiers of plant tissue culture. Int. Assoc. Plant Tissue Culture, Calgary.

Dvořák, J. 1977. Transfer of leaf rust resistance from *Aegilops speltoides* to *Triticum aestivum*. Can. J. Genet. Cytol. 19:133–141.

Dyck, P.L., and E.R. Kerber. 1970. Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from *Aegilops squarrosa*. Can. J. Genet. Cytol. 12:175–180.

Eapen, S., and P.S. Rao. 1982. Organogenesis and plantlet formation from callus cultures of different cultivars of bread wheat (*Triticum aestivum*). Proc. Indian Natl. Sci. Acad. Part B 48 (3): 371–377.

----, and ----. 1984. Spontaneous and induced variation in tissue cultures and regenerated plants of bread wheat. p. 461–467. *In* L.A. Withers and P.G. Alderson (ed.) Plant tissue culture and its agricultural applications. Butterworths, London.

Endo, T.R. 1982. Gametocidal chromosomes of three *Aegilops* species in common wheat. Can. J. Genet. Cytol. 24:201–206.

Evans, D.A., and W.R. Sharp. 1983. Single gene mutations in tomato plants regenerated from tissue culture. Science 221:949–951.

----, and ----, and H.P. Medina-Filho. 1984. Somaclonal and gametoclonal variation. Am. J. Bot. 71:759–774.

Falk, D.E., and K.J. Kasha. 1981. Comparison of the crossability of rye (*Secale cereale*) and *Hordeum bulbosum* onto wheat (*Triticum aestivum*). Can. J. Genet. Cytol. 23:81–88.

FAO/IAEA. 1972–1984. Mutation Breeding Newsletter. Vol. 1–21. IAEA, Vienna.

Fasoulas, A. 1973. A new approach to breeding superior yielding varieties. Aristotelian Univ. Dep. Genet. Plant Breeding Pub. 3. Thessalonika, Greece.

Favret, E.A. 1981. Basic concepts on induced mutagenesis for disease reaction. p. 55–66. *In* Mutation breeding for disease resistance. Proc. of Panel on Mutation Breeding for Disease Resistance, Vienna, Austria. 2–6 Oct. 1979. IAEA, Vienna. STI/PUB/271.

----. 1976. Breeding for disease resistance using induced mutations. p. 95–111. *In* Induced mutations in cross-breeding. Proc. of an Advisory Group, Vienna, Austria. 13–17 Oct. 1975. IAEA, Vienna. STI/PUB/447.

----, R.M. Solari, and L.E. Manghers. 1984. Genetics of prolamin synthesis in cereal endosperms and its implication in plant breeding. p. 301–320. *In* Cereal grain protein improvement. Proc. Final Res. Coord. Meet. for Cereal Grain Protein Improvement, Vienna, Austria. 6–10 Dec. 1982. IAEA, Vienna. STI/PUB/664.

Feldman, M., and E.R. Sears. 1981. The wild gene resources of wheat. Sci. Am. 244:102–112.

Finch, R.A., and M.D. Bennett. 1980. Mitotic and meiotic chromosome behavior in new hybrids of *Hordeum* with *Triticum* and *Secale*. Heredity 44:201–209.

Fisher, R.A., and Z. Kertesz. 1976. Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. Crop Sci. 16:55–59.

Fowler, W.R., and E.G. Heyne. 1955. Evaluation of bulk hybrid tests for predicting performance of pure line selections in hard red winter wheat. Agron. J. 47:430–434.

Franckowiak, J.D., S.S. Maan, and N.D. Williams. 1976. A proposal for hybrid wheat utilizing *Aegilops squarrosa* L. cytoplasm. Crop Sci. 16:725–728.

Frydenberg, O., and P. Jacobsen. 1966. The mutation and segregation frequencies in different spike categories after chemical treatment of barley seeds. Hereditas 55:227–248.

Fukasawa, H. 1953. Studies on restoration and substitution of nucleus in *Aegilotricum*. I. Appearance of male-sterile durum in substitution crosses. Cytologia 18:167–175.

Gale, M.D., and S. Youssefian. 1985. Dwarfing genes in wheat. p. 1–35. *In* G.E. Russell (ed.) Progress in plant breeding. Vol. 1. Butterworth and Co., London.

Gaul, H. 1964. Mutations in plant breeding. Radiat. Bot. 4:155–232.

----, and K. Aastviet. 1966. Induced variability of culm length in different genotypes of hexaploid wheat following X-irradiation and EMS treatment. Savrem. Poljopr. 14:253–276.

Ghaderi, A., E.H. Everson, and C.E. Cress. 1980. Classification of environments and genotypes in wheat. Crop Sci. 20:707–710.

Ghiasi, H., K.A. Lucken, and J.J. Hammond. 1982. Selection procedures for developing fertility restorer lines in wheat. Crop Sci. 22:523–527.

Gill, B.S., L.E. Browder, J.H. Hatchett, T.L. Harvey, T.J. Martin, W.J. Raupp, and J.G. Waines. 1983. Disease and pest resistance in wild wheats. p. 785–792. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December Plant Germ-Plasm Inst., Fac. Agric., Kyoto University, Kyoto.

----, and J.G. Waines. 1978. Paternal regulation of seed development in wheat hybrids. Theor. Appl. Genet. 51:265–270.

Gill, K.S., G.S. Nanda, G. Singh, and S.S. Aujla. 1981. KSML3 wheat multiline variety for Punjab, India. p. 3–4. *In* Indian multilines. CIMMYT, Mexico.

Gilmore, E.C. 1964. Suggested method of using reciprocal recurrent selection in some naturally self-pollinated species. Crop Sci. 4: 323–325.

Giorgi, B. 1978. A homoeologous pairing mutant isolated in *Triticum durum* cv. Capelli. Mut. Breed. Newsl. 11:4–5.

----. 1986. Comparison of gibberellin insensitive and responsive semidwarf F_4 lines of durum wheat. *In* Evaluation of semi-dwarf cereal mutants for cross breeding. Proc. 4th FAO/IAEA Res. Coord. Meet., Casaccia, Rome, Italy. 16–20 Dec. 1985. IAEA, Vienna. In press.

----, F. Barbera, O. Bitti, and G. Cavicchioni. 1984. Yield performance of F_3 progenies from a durum wheat cross involving two different semidwarfing genes: *Rht* 1 and *SD* mutation. p. 91–99. *In* Semi-dwarf cereal mutants and their use in cross-breeding Vol. II. Proc. Res. Coord. Meet. on Evaluation of Semi-dwarf Cereal Mutants for Cross Breeding, Davis, California. 30 Aug.-3 Sept. 1982. IAEA, Vienna. TECDOC-307.

----, and C. Mosconi. 1982. Short-straw mutants and other dwarfing gene sources used for the improvement of wheats and barley in Italy. p. 53–64. *In* Semi-dwarf cereal mutants and their use in cross-breeding. Proc. of a Res. Coord. Meet., Vienna, Austria. 2–6 Mar. 1981. IAEA, Vienna. TECDOC-268.

Grafius, J.E. 1965. Short cuts in plant breeding. Crop Sci. 5:377.

Grama, A., and Z.K. Gerechter-Amitai. 1974. Inheritance of resistance to stripe rust (*Puccinia striiformis*) in crosses between wild emmer (*Triticum dicoccoides*) and cultivated tetraploid and hexaploid wheats. II. *Triticum aestivum.* Euphytica 23:393–398.

Groose, R.W., and E.T. Bingham. 1984. An unstable anthocyanin mutation recovered from tissue culture of alfalfa. Agron. Abstr. American Society of Agronomy, Madison WI, p. 68.

Groth, J.V. 1976. Multilines and "super races": A simple model. Phytopathology 66:937–939.

Gustafsson, A., and U. Lundqvist. 1981. Mutations and parallel variation. p. 85–109. *In* Induced mutations—a tool in plant research. Proc. Symp. on Induced Mutations as a Tool for Crop Plant Improvement, Vienna, Austria. 9–13 Mar. 1981. IAEA, Vienna. STI/PUB/591.

Hadley, H.H., and S.J. Openshaw. 1980. Interspecific and intergeneric hybridization. p. 133–159. *In* W.R. Fehr and H.H. Hadley (ed.) Hybridization in crop plants. American Society of Agronomy, Madison, WI.

Halloran, G.M. 1974. *Ophiobolus graminis* resistance in the genera *Agropyron* and *Secale* and its possible significance to wheat breeding. Euphytica 23:225–235.

Hao, S., M. He, Z. Xu, M. Zou, H. Hu, Z. Xi, and J. Ouyang. 1980. Formation of 'mini-microspore' in anther-derived haploids of *Triticum aestivum* and its possible use. p. 389–392. *In* F. Sala et al. (ed.) Plant cell culture: results and perspectives. Elsevier/North Holland Biomedical Press, Amsterdam/New York.

Harrington, J.B. 1940. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Can. J. Res. Sec. C 18:578–584.

Harvey, T.H., T.J. Martin, and R.W. Livers. 1980. Resistance to biotype C greenbug *Shizaphis graminum* in synthetic hexaploid wheats derived from *Triticum tauschii*. J. Econ. Entomol. 73:387–389.

Hatchett, J.H., T.J. Martin, and R.W. Livers. 1981. Expression and inheritance of resistance to Hessian fly in synthetic hexaploid wheats derived from *Triticum tauschii* (Coss) Schmal. Crop Sci. 21:731–734.

Hayes, H.K., J.H. Parker, and C. Kurtzweil. 1920. Genetics of rust resistance in crosses of varieties of *Triticum vulgare* with varieties of *T. durum* and *T. dicoccum*. J. Agric. Res. 19:523–542.

Hayward, C.F. 1975. The status of and prospects for hybrid winter wheat. p. 84–89. *In* Proc. 2nd Int. Winter Wheat Conf. Zagreb, Yugoslavia, 9–19 June. USDA, USAID, and University of Nebraska, sponsors.

He, D., and J.W. Ouyang. 1982. Studies on pollen grain albino plantlets. I. Gene mutation—not the main cause of albino plantlets. p. 30. Annu. Rep. Inst. Genet. Acad. Sinica.

Heiner, R.E., and F.A. Elsayed. 1974. Registration of MN6616 M wheat germ plasm. Crop Sci. 14:342–343.

Henry, Y., and J. De Buyser. 1981. Float culture of wheat anthers. Theor. Appl. Genet. 60:77–90.

Hermelin, T. 1984. Induction and selection of protein mutants in spring wheat at the IAEA Seibersdorf Laboratory. p. 17–24. *In* Cereal grain protein improvement. Proc. of Final Res. Coord. Meet. for Cereal Grain Protein Improvement, Vienna, Austria. 6–10 Dec. 1982. IAEA, Vienna. STI/PUB/664.

Hess, D., H. Maier, M. Scholl, and J. Kemmer. 1983. Nitrogenase activity induced by wheat plants: competition experiments between *Rhizobium* 32H1, *Rhizobium japonicum*, and *Escherichia coli*. Z. Pflanzenphysiol. 11:213–221.

Heszky, L., and J. Mesch. 1976. Anther culture investigations in cereal gene bank collection. Z. Pflanzenzuecht. 77:187–197.

Heyne, E.G., and E.S. Smith. 1967. Wheat breeding. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:269–306.

Heyser, J.W., M.W. Nabors, C. MacKinnon, T.A. Dykes, K.J. Demott, D.C. Kautzman, and A. Mujeeb-Kazi. 1985. Long-term, high frequency plant regeneration and the induction of somatic embryogenesis in callus cultures of wheat (*Triticum aestivum* L.) Z. Pflanzenzuecht. 94:218–233.

Hondelmann, W. 1978. Wheat germplasm collection, conservation and utilization through international cooperation. p. 149–155. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., Indian Soc. Genet. Plant Breed., New Delhi, India.

Hu, Han, T. Hsi, C. Tseng, T. Ouyang, and C. Ching. 1978. Application of anther culture to crop plants. p. 123–130. *In* T.A. Thorpe (ed.) Frontiers of plant tissue culture. Calgary, Canada.

Hughes, W.G., and J.J. Bodden. 1978. An assessment of the production and performance of F_1 hybrid wheats based on *Triticum timopheevii* cytoplasm. Theor. Appl. Genet. 53:219–228.

Hull, H. M., L.N. Wright, and C.A. Bleckmann. 1978. Epicuticular wax ultrastructure among lines of *Eragrostis lehmanniana* Nees developed for seedling drouth tolerance. Crop Sci. 18:699–704.

IAEA. 1977. Manual on mutation breeding. 2nd ed. IAEA, Vienna.

Islam, A.K.M.R., and K.W. Shepherd. 1981. Production of disomic wheat–barley chromosome addition lines using *Hordeum bulbosum* crosses. Genet. Res. 37:215–219.

----, K.W. Shepherd, and D.H.B. Sparrow. 1981. Isolation and characterization of euplasmic wheat-barley chromosome addition lines. Heredity 46:161–174.

Jan, C.-C., J. Dvořák, C.O. Qualset, and K.M. Soliman. 1981. Selection and identification of a spontaneous alien chromosome translocation in wheat. Genetics 98:389–398.

----, C.O. Qualset, and H.E. Vogt. 1974. Chemical induction of sterility in wheat. Euphytica 23:74–85.

Jensen, N.F. 1952. Intra-varietal diversification in oat breeding. Agron. J. 44:30–34.

----. 1970. A diallel selective mating system for cereal breeding. Crop Sci. 10:629–635.

Jinks, J.L., and H.S. Pooni. 1981. Properties of pure breeding lines produced by dihaploidy, single seed descent and pedigree breeding. Heredity 46:391–395.

Johnson, B.B., and H. Nguyen. 1984. Somaclonal variation in spike characteristics of wheat. *In* Proc. Int. Symp. Genet. Manipulation in Crops. Beijing. (Abstr.)

Johnson, D.A., R.A. Richards, and N.C. Turner. 1983. Yield, water relations, gas exchange, and surface reflectances of near isogenic wheat lines differing in glaucousness. Crop Sci. 23:318–325.

---- M.L. Tonnet, and R.A. Richards. 1984. Estimation of epicuticular wax amounts in wheat using wide line proton magnetic resonance. Crop Sci. 24:679–682.

Johnson, K.D. 1984. Chemical hybridizing activity of SD 84811 on hard red spring wheat. M.S. thesis. North Dakota State Univ., Fargo.

Johnson, R.R., and C.M. Brown. 1978. Use of DPX 3778 to produce hybrid wheat seed. Crop Sci. 18:1026–1028.

Johnson, V.A. 1977. Small grains. Twenty-third Farm Seed Conf., Amer. Seed Trade Assoc. p. 27–34.

Joppa, L.R., R.G. Timian, and N.D. Williams. 1980. Inheritance of resistance to greenbug toxicity in an amphiploid of *Triticum turgidum-T. tauschii*. Crop Sci. 20:343–344.

Jordan, M.C. 1984. Somaclonal variation in Triticale (X Triticosecale Wittmack) cv. 'Corman'. M.Sc. thesis, Univ. of Manitoba.

Joshi, B.C., and D. Singh. 1979. Introduction of alien variation into bread wheat. p. 342–348. *In* Proc. 5th Int. Wheat Genet. Symp., New Delhi.

Joshua, D.C., and C.R. Bhatia. 1984. Identification of mutants at different phenotypic levels. p. 121–131. *In* Selection in mutation breeding. Proc. Consult. Meet., Vienna, Austria. 21–25 June 1982. IAEA, Vienna. STI/PUB/665.

Jošt, M., and K.A. Lucken. 1983. Stability of fertility restoration in some F_1 spring and winter wheat hybrids grown in the International Wheat Restorer Germplasm Screening Nursery. p. 675–682. *In* Sakao Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan, 28 November–3 December. Plant Germ-plasm Inst., Faculty of Agric., Kyoto University.

Kapulnik, Y., S. Sarig, I. Nur, and Y. Okon. 1983. Effect of *Azospirillum* inoculation on yield of field-grown wheat. Can. J. Microbiol. 29:895–899.

Kar, G.N., S.N. Chakrabarti, and A.B. Prasad. 1978. Improvement of bread wheat through mutation breeding. Wheat Newsl. 24:62–63.

Kasha, K.J. 1974. Haploids from somatic cells. p. 67–87. *In* K.J. Kasha (ed.) Haploids in higher plants. Univ. of Guelph, Guelph, Canada.

Kerber, E.R. 1983. Suppression of rust resistance in amphiploids of *Triticum*. p. 813–817. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ. Plasm Inst., Fac. Agric., Kyoto University, Kyoto.

----, and P.L. Dyck. 1969. Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from *Aegilops squarrosa*. Can. J. Genet. Cytol. 11:639–647.

----, and ----. 1973. Inheritance of stem rust resistance transferred from diploid wheat (*Triticum monococcum*) to tetraploid and hexaploid wheat and chromosome location of the gene involved. Can. J. Genet. Cytol. 15:397–409.

----, and ----. 1978. Resistance to stem and leaf rust of wheat in *Aegilops squarrosa* and transfer of a gene for stem rust resistance to hexaploid wheat. p. 358–364. *In* S. Ramanujam (ed.) 5th Int. Wheat Genet. Symp. Indian Society of Genetics and Plant Breeding, New Delhi, India.

----, and G.J. Green. 1980. Suppression of stem rust resistance in the hexaploid wheat, cv. Canthatch by chromosome 7DL. Can. J. Bot. 58:1347–1350.

Khiznjak, N.A. 1937. Wheat-*Agropyron* amphidiploids—A new useful fodder crop plant. Sel. Semenovod. [Plant Breed. and Seed Production] 11:56–57. (Plant Breed. Abstr. 8:1495).

Kibirige-Sebunya, I., and D.R. Knott. 1983. Transfer of stem rust resistance to wheat from

an *Agropyron* chromosome having a gametocidal effect. Can. J. Genet. Cytol. 25:215–221.

Kihara, H. 1937. Genomanalyse bei *Triticum* und *Aegilops*. VII. Kurze Uberscicht uber die Ergebnisse der Jahre 1934–1936. Mem. Coll. Agric., Kyoto Imp. Univ. 41:1–61.

———. 1951. Substitution of nucleus and its effect on genome manifestations. Cytologia 16:177–193.

——— (ed.) 1954. wheat research. 2nd ed. Yokemdo Co., Tokyo, (In Japanese.).

———, and K. Tsunewaki. 1962. Use of an alien cytoplasm as a new method of producing haploids. Jpn. J. Genet. 37:310–313.

———, K. Yamashita, and M. Tanaka. 1965. Morphological physiological, genetical and cytological studies in *Aegilops* and *Triticum* collected from Pakinstan, Afghanistan and Iran. p. 1–118. *In* K. Yamashita (ed.). Cultivated plants and their wild relatives. Kyoto Univ., Kyoto, Japan.

Kilpatrick. R.A., and J.G. Moseman. 1978. Fifty years of national and international uniform wheat rust nurseries. p. 1039–1048. *In* S. Ramanujam (ed.). Proc. 5th Int. Wheat Genet. Symp. Indian Society of Genetics and Plant Breeding, New Delhi, India.

Kimber, G. 1979. Amphiploids as a genetic resource in *Triticeae*. Indian J. Genet. Plant Breed. 39:133–137.

———. 1984. Technique selection for the introduction of alien variation in wheat. Z. Pflanzenzuecht. 92:15–21.

———, and M. Abubakar. 1979. Wheat hybrid information system. Cereal Res. Commun. 7:257–260.

———, and P.J. Sallee. 1976. A hybrid between *Triticum timopheevii* and *Hordeum bogdanii*. Cereal Res. Commun. 4:33–37.

Kleinhofs, A., T. Kuo, and R.L. Warner. 1980. Characterization of nitrate reductase deficient barley mutants. Mol. Gen. Genet. 177:421–425.

———, W.M. Owais, and R.A. Nilan. 1978. Azide. Mutat. Res. 55:165–195.

———, C. Sander, R.A. Nilan, and C.F. Konzak. 1974. Azide mutagenicity—Mechanism and nature of mutants produced. p. 195–199. *In* Polyploidy and induced mutations in plant breeding. Proc. Meet. on Mutation and Polyploidy and Res. Coord. Meet. on Improvement of Mutation Breeding Tech., Bari, Italy. 2–10 October 1972. IAEA, Vienna. STI/PUB/359.

Knobloch, I.W. 1968. A check list of crosses in the Gramineae. Stechert-Hofner Service Agency, New York.

Knott, D.R. 1961. The inheritance of rust resistance. VI. The transfer of stem rust resistance from *Agropyron elongatum* to common wheat. Can. J. Plant Sci. 41:109–123.

———. 1971. The transfer of genes for disease resistance from alien species to wheat by induced translocations. p. 67–77. *In* Mutation breeding for disease resistance. IAEA, Vienna.

———. 1972. Effects of selection for F_2 plant yield on subsequent generations in wheat. Can. J. Plant Sci. 52:721–726.

———. 1979. Selection for yield in wheat breeding. Euphytica 28:37–40.

———. 1979. The transfer of genes for rust resistance to wheat from related species. p. 354–357. *In* Proc. 5th Int. Wheat Genet. Symp., New Delhi, India.

———, and J. Dvořák. 1981. Agronomic and quality characteristics of wheat lines with leaf rust resistance derived from *Triticum speltoides*. Can. J. Genet. Cytol. 23:475–480.

———, and J. Kumar. 1975. Comparison of early generation yield testing and a single seed descent procedure in wheat breeding. Crop Sci. 15:295–299.

Kobayshi, M., and K. Tsunewaki. 1980. Haploid induction and its genetic mechanism in alloplasmic common wheat. J. Hered. 71:9–14.

Kolattukudy, P.E. 1980. Biopolyester membrane of plants: Cutin and suberin. Science 208:990–1000.

Konzak, C.F. 1981. Induced mutations for genetic analyses and improvement of wheat, p. 469–488. *In* Induced mutations—a tool in crop plant research. Proc. Symp. on Induced

Mutations as a Tool for Crop Improvement, Vienna, Austria. 9–13 March. IAEA, Vienna. STI/PUB/591.

----. 1982. Evaluation and genetic analysis of semi-dwarf mutants of wheat. p. 25–37. *In* Semi-dwarf cereal mutants and their use in cross-breeding. Proc. of Res. Coord. Meet., Vienna. 2–6 Mar. 1981. IAEA, Vienna. TECDOC-268.

----. 1984. Role of induced mutations. p. 216–292. *In* P.B. Vose and S. Blixt (ed.) Crop breeding, a contemporary basis. Pergamon Press, New York.

----. 1986. Genetic analysis, genetic improvement and evaluation of induced semi-dwarf mutants in wheat. *In* Evaluation of Semi-dwarf Cereal Mutants for Cross Breeding. Proc. 4th FAO/IAEA Res. Coord. Meet., Casaccia, Rome, Italy. 16–20 Dec. 1985. IAEA, Vienna. In press.

----, A. Kleinhofs, and S.E. Ullrich. 1984a. Induced mutations in seed propagated crops. p. 13–72. *In* J. Janick (ed.) Plant breeding reviews. Vol. 2. AVI Publishing Co., Westport, CT.

----, R.A. Nilan, J. Wagner, and R.J. Foster. 1965. Efficient chemical mutagenesis. p. 49–70. *In* The use of induced mutations in plant breeding. Rep. of Meet. FAO/IAEA, Rome, Italy. 25 May–1 June 1964. Pergamon Press, Oxford.

----, M.R. Wilson, and P.A. Franks. 1984b. Progress in the evaluation, use in breeding, and genetic analysis of semidwarf mutants of wheat. p. 39–50. *In* Semi-dwarf cereal mutants and their use in cross-breeding. Vol. II. Proc. of Res. Coord. Meet. on Evaluation of Semi-dwarf Cereal Mutants for Cross Breeding, Davis, California. 30 Aug.–3 Sep. 1982. IAEA, Vienna. TECDOC-307.

Kostoff, D. 1940. Fertility and chromosome length. Correlations between chromosome length and viability of gemetes in autopolyploid plants. J. Hered. 31:33–34.

----, and N. Arutiunova. 1937. Studies on the polyploid plants *Triticum-Haynaldia* hybrids with special reference to the amphidiploids *Triticum dicoccum* × *Haynaldia villosa.* Curr. Sci. 5:414–415.

Larik, A.S., K.A. Siddiqui, H.M.I. Hafiz, and M.H. Arain. 1984. Evaluation of wheat mutants for days to maturity. Wheat Inf. Serv. 58:22–24.

Larkin, P.J., S.A. Ryan, R.I.S. Brettell, and W.R. Scowcroft. 1984. Heritable somaclonal variation in wheat. Theor. Appl. Genet. 67:443–455.

----, and W.R. Scowcroft. 1981. Somaclonal variation—A novel source of variability from cell cultures for plant improvement. Theor. Appl. Genet. 60:197–214.

Larson, R.I., and J.L. Neal, Jr. 1978. Selective colonization of the rhizosphere of wheat by nitrogen-fixing bacteria. p. 331–342. *In* U. Granhall (ed.) Environmental role of nitrogen-fixing blue-green algae and asymbiotic bacteria. Ecol. Bull. (Stockholm) 26.

Law, C.N., R.C. Gaines, R. Johnson, and A.J. Worland. 1978. The application of aneuploid technique to a study of stripe rust resistance in wheat. p. 427–436. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genetics Symp., New Delhi, 1978. Indian Soc. Genet. and Plant Breeding.

Lbova, M.I., and I.V. Cherniy. 1979. Monosomic analysis of some morphological characters of a spring wheat Novosibirskaya 67 and its initial forms. Genetika 25:1439–1448.

Leighty, C.E., and W.J. Sando. 1928. Natural and artificial hybrids of a Chinese wheat and rye. J. Hered. 19:23–27.

----, ----, and J.W. Taylor. 1926. Intergeneric hybrids in *Aegilops, Triticum*, and *Secale.* J. Agric. Res. 33:101–141.

Lein, A. 1943. The genetical basis of the crossability between wheat and rye. Z. Indukt. Abstam-u-Vererbungsl. 81:28–59. (Plant Breed. Abstr. 14:1197).

Liang, G.H., N. Sangduen, E.G. Heyne, and R.G. Sears. 1982. Polyhaploid production through anther culture in common wheat. J. Hered. 73:360–364.

----, R.C. Wang, C.L. Niblett, and E.G. Heyne. 1979. Registration of B-6-37-1 wheat germplasm. Crop Sci. 19:421.

Limin, A.E., and D.B. Fowler. 1981. Cold hardiness of some relatives of hexaploid wheat. Can. J. Bot. 59:572–573.

----, and ----. 1985. Cold hardiness in *Triticum* and *Aegilops* species. Can. J. Plant Sci. 65:71–77.

Line, R.F., C.F. Konzak, and R.E. Allan. 1974. Evaluating resistance to *Puccinia striiformis* in wheat. p. 123–133. *In* Induced mutations for disease resistance in crop plants. Proc. of Res. Coord. Meet. on Induced Mutations for Disease Resistance in Crop Plants, Novi Sad, Yugoslavia. 4–8 June 1973. IAEA, Vienna. STI/PUB/388.

Livers, R.W. 1964. Fertility restoration and its inheritance in cytoplasmic male sterile wheat. Science 144:420.

Loegering, W.Q., and E.R. Sears. 1963. Distorted inheritance of stem-rust resistance of Timstein wheat caused by a pollen-killing gene. Can. J. Genet. Cytol. 5:65–72.

Loffler, C.M., R.H. Busch, and J.V. Wiersma. 1983. Recurrent selection for grain protein percentage in hard red spring wheat. Crop Sci. 23:1097–1101.

Love, R.M. 1947. Interspecific and intergeneric hybridization in forage crop improvement. J. Am. Soc. Agron. 39:41–47.

Maan, S.S. 1975. Cytoplasmic variability and speciation in Triticinae. p. 255–281. *In* M.K. Wali (ed.) Prairie: A multiple view. University of North Dakota Press, Grand Forks.

———. 1976. Cytoplasmic homology between *Aegilops squarrosa* L. and *A. cylindrica* Host. Crop Sci. 16:757–761.

———. 1977. Cytoplasmic control of cross-incompatibility, and zygotic and sporophytic sterility in interspecific hybrids. p. 201–214. *In* E. Sanchez-Monge and F. Garcia-Olmedo (ed.) Proc. 8th EUGARPIA Congr., Madrid, Spain.

———, and K.A. Lucken, and J.M. Bravo. 1984. Genetic analyses of male-fertility restoration in wheat. I. Chromosomal location of *Rf* genes. Crop Sci. 24:17–20.

———, and E.U. McCracken. 1968. Meiotic instability of common wheat strains derived from *Triticum timopheevi* Zhuk. crosses. Euphytica 17:445–450.

———, and T. Sasakuma. 1977. Fertility of amphihaploids in Triticinae. J. Hered. 68:87–94.

———, and N.D. Williams. 1984. An EMS induced dominant allele for male-sterility transferred to euplasmic wheat. Crop Sci. 24:851–852.

MacKey, J. 1956. Mutation breeding in Europe. p. 141–156. *In* Genetics in plant breeding. Brookhaven Symp. in Biol. No. 9, Upton, NY. 21–23 May. Associated Universities, Inc., Upton, New York.

———. 1967. Physical and chemical mutagenesis in relation to ploidy level. p. 185–197. *In* H. Stubbe et al. (ed.) Induzierte Mutationen und ihre Nutzung. Erwin Bauer-Gedachtnisvorlesungen IV, Gatersleben, 19–24 June 1966. Akademie-Verlag, Berlin.

———. 1981a. Mutations as means for analyzing polyploid systems. p. 143–151. *In* Induced Mutations—A tool for crop plant research. Proc. of Int. Symp. on Induced Mutations as a Tool for Crop Plant Improvement, Vienna, Austria. 9–13 March. IAEA, Vienna. STI/PUB/591.

———. 1981b. The value of induced mutation research in advancing knowledge in genetics. p. 3–22. *In* Induced mutations—A tool for crop plant research. Proc. of Int. Symp. on Induced Mutations as a Tool for Crop Plant Improvement, Vienna, Austria. 9–13 March. IAEA, Vienna. STI/PUB/591.

———. 1984. Selection problems and objectives in mutation breeding. p. 35–48. *In* Selection in mutation breeding. Proc. Consult. Meet., Vienna, Austria. 21–25 June 1982. IAEA, Vienna. STI/PUB/665.

Maddock, S.E., V.A. Lancaster, R. Risiott, and J. Franklin. 1983. Plant regeneration from cultured immature embryos and inflorescences of 25 cultivars of wheat (*Triticum aestivum*). J. Exp. Bot. 34:915–926.

Martens, J.L., P.D. Brown, R.I.H. McKenzie, and D.E. Harder. 1983. Development of resistance to *Puccinia graminis avenae* in *Avena sativa* by mutagen treatment. p. 105–110. *In* Induced mutations for disease resistance in crop plants Vol. II. Proc. Res. Coord. Meet., Risø, 15–19 June 1981. IAEA, Vienna. STI/PUB/633.

Martin, A. 1983. Cytology and morphology of the hybrid *Hordeum chilense* × *Aegilops squarrosa*. J. Hered. 74:487.

———, and V. Chapman. 1977. A hybrid between *Hordeum chilense* and *Triticum aestivum*. Cereal Res. Commun. 5:365–368.

———, and E.S. Laguna. 1980. A hybrid between *Hordeum chilense* and *Triticum turgidum*. Cereal Res. Commun. 8:349–354.

Martin, T.J., T.L. Harvey, and J.H. Hatchett. 1982. Registration of greenbug and Hessian fly resistant wheat germplasm. Crop Sci. 22:1089.

McCoy, T.J., R.L. Phillips, and H.W. Rines. 1982. Cytogenetic analysis of plants regenerated from oat (*Avena sativa*) tissue cultures: High frequency of partial chromosome loss. Can. J. Genet. Cytol. 24:37–50.

McFadden, E.S. 1930. A successful transfer of emmer characters to *vulgare* wheat. J. Am. Soc. Agron. 22:1020–1034.

----, and E.R. Sears. 1946. The origin of *T. spelta* and its free-threshing hexaploid relatives. J. Hered. 37:81–89.

McGinnis, R.C., and L.H. Shebeski. 1968. The reliability of single plant selection for yield in F_2. p. 410–415. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Canberra, Australia. 5–9 August. Australian Academy of Science, Canberra.

McGuire, P.E., and J. Dvořák. 1981. High salt-tolerance potential in wheatgrasses. Crop Sci. 21:702–705.

McHughen, A. 1983. Rapid regeneration of wheat *in vitro*. Ann. Bot. 51:851–853.

McIntosh, R.A. 1973. A catalogue of gene symbols for wheat. p. 893–937. *In* E.R. Sears and L.M. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

----. and J. Gyarfas. 1971. *Triticum timopheevii* as a source of resistance to wheat stem rust. Z. Pflanzenzuecht. 66:240–248.

McNeal, F.H., C.F. McGuire, and M.A. Berg. 1978. Recurrent selection for grain content in spring wheat. Crop Sci. 18:779–782.

McRae, D. Harold. 1985. Advances in chemical hybridization. Plant Breeding Rev. 3:169–191.

McVetty, P.B.E., and L.E. Evans. 1980. Breeding methodology in wheat. I. Determination of characters measured on F_2 spaced plants for yield selection in spring wheat. Crop Sci. 20:583–586.

Merkle, O.G., and K.J. Starks. 1985. Resistance of wheat to yellow sugarcane aphid (Homoptera: Aphididae). J. Econ. Entomol. 78:127–128.

Mettin, D., W.D. Bluthner, and G. Schlegel. 1973. Additional evidence on spontaneous 1B/1R wheat–rye substitutions and translocations. p. 179–184. *In* Proc. 4th Intern. Wheat Genet. Symp., Columbia, MO.

Micke, A. 1979. Use of induced mutations to alter the ontogenetic pattern of crop plants. p. 1–23. *In* Crop improvement by induced mutation. Gamma Field Symp. 18, Ohmiya, Japan. 21–22 May.

----. 1984. Introduction. p. 1–4. *In* Selection in mutation breeding. Proc. Consult. Meet., Vienna, Austria. 21–25 June 1982. IAEA, Vienna. STI/PUB/665.

----, and B. Donini. 1982. Use of induced mutations for the improvement of seed propagated crops. p. 2–9. *In* Induced Variability in Plant Breeding. Proc. Int. Symp. Sect. Mutation and Polyploidy. Wageningen, Netherlands.

Miller, J.F., and K.A. Lucken. 1977. Gametocidal properties of RH-531, RH-532, RH-2956, and RH-4667. Euphytica 26:103–112.

Miller, T.E., S.M. Reader, and V. Chapman. 1982. The addition of *Hordeum chilense* chromosomes to wheat. p. 79–81. *In* Induced Variability in Plant Breeding. Proc. Int. Symp. Mutation and Polyploidy. Wageningen, Netherlands.

Mitchell, J.W., R.J. Baker, and D.R. Knott. 1982. Evaluation of honeycomb selection for single plant yield in durum wheat. Crop Sci. 22:840–843.

Morris, R., and E.R. Sears. 1967. The cytogenetics of wheat and its relatives, *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and Wheat Improvement. 1st ed. Agronomy 13:19–87.

Moseman, J.G., R.A. Kilpatrick, and W.M. Porter. 1978. Evaluation and documentation of pest resistance in wheat germplasm collections. p. 143–148. *In* S. Ramanujam (ed.). Proc. 5th Int. Wheat Genet. Symp. Indian Society of Genetics and Plant Breeding, New Delhi, India.

Mujeeb-Kazi, A., and R. Rodriguez. 1981. An intergeneric hybrid of *Triticum aestivum* × *Elymus giganteus*. J. Hered. 72:253–256.

Mukai, Y. 1981. Genetic studies of the wheat haploids induced by alien cytoplasms. Mem. Osaka Kyoiki Univ., Ser. III, 30:31–55.

----, and K. Tsunewaki. 1979. Basic studies on hybrid wheat breeding. VIII. A new male sterility-fertility restoration system in common wheat utilizing the cytoplasms of *Aegilops kotshyi* and *Ae. variabilis*. Theor. Appl. Genet. 54:153–160.

Muramatsu, M., S. Kaneta, R. Ikeda, T. Uetsuki, and K. Takahashi. 1983. Hybridization experiment of Japanese indigenous *Agropyron* (Roegneria) species with hexaploid wheat and cytogenetic result of some of the F_1, BF_1, and amphiploid plants. p. 1041–1048. *In* S. Sakmoto (ed.). Proc. 6th Int. Wheat genet. Symp., Kyoto Univ., Kyoto, Japan.

Murashige, T. 1977. Current status of plant cell and organ cultures. Hortic. Sci. 12:127–130.

----, and F. Skoog. 1962. A revised meduim for rapid growth and bioassays with tobacco tissue culture. Physiol. Plant. 15:473–497.

Nabors, M.W., J.W. Heyser, T.A. Dykes, and K.J. DeMott. 1983. Long-duration, high-frequency plant regeneration from cereal tissue cultures. Planta 157:385–391.

Nass, H.G. 1979. Selecting superior spring wheat crosses in early generations. Euphytica 28:161–167.

----. 1980. Harvest index as a selection criterion for grain yield in two spring wheat crosses grown at two population densities. Can. J. Plant Sci. 60:1141–1146.

Nelson, A.D., L.E. Barber, J. Tjepkeman, S.A. Russell, R. Powelson, H.J. Evans, and R.J. Seidler. 1976. Nitrogen fixation associated with grasses in Oregon. Can. J. Microbiol. 22:523–530.

Nilan, R.A., and C.E. Muir. 1967. Registration of Luther barley. Crop Sci. 7:278.

Norstog, K. 1973. A new synthetic medium for the culture of premature barley embryos. In vitro 8:307–308.

Nyquist, W.E. 1962. Differential fertilization in the inheritance of stem rust resistance in hybrids involving a common wheat strain derived from *Triticum timopheevi*. Genetics 47:1109–1124.

O'Brien, L., R.J. Baker, and L.E. Evans. 1978. Response to selection for yield in F_3 of four wheat crosses. Crop Sci. 18:1029–1033.

Okamoto, M. 1957. Asynaptic effect of chromosome V. Wheat Inf. Serv. 5:6.

Okon, Y. 1982. *Azospirillum*. Phytoparasitica 10:2.

Orshinsky, B.R., and A. McHughen. 1984. Callus initiation and plantlet formation in two wheat cultivars. IAPTC (Canada) 1st Plant Genetic Engineering Workshop. Saskatoon, Sask., Canada (Abstr.).

Ouyang, J.W., S.M. Zhou, and S.E. Jia. 1983. The response of anther culture to culture temperature in *Triticum aestivum*. Theor. Appl. Genet. 66:101–109.

Ozias-Akins, P., and I.K. Vasil. 1982. Plant regeneration from cultured immature embryos and inflorescences of *Triticum aestivum* L. (wheat): Evidence for somatic embryogenesis. Protoplasma 100:95–105.

Padilla, J.A., and A. Martin. 1983. New hybrids between *Hordeum chilense* and tetraploid wheats. Cereal Res. Commun. 11:5–7.

Panayotov, I., and K. Gotzov. 1981. Utilization of *Ae. variabilis* and *Ae. kotschyi* cytoplasms and Avrora nucleus for hybrid wheat production. Annu. Wheat Newsl. 27:42–43.

----, P. Popov, and K. Gotzov. 1975. Interactions between the nucleus of *Triticum aestivum* and the cytoplasms of some *Triticum* and *Aegilops* species. Genet. Sel. 8:157–165.

Parodi, P.C., and I.M. Nebreda. 1982a *Triticum aestivum*. Carolina. Mutat. Breed. Newsl. 19:18.

----, and ----. 1982b. Testing, cross-breeding, induction and nutritional evaluation of wheat and triticale mutants. p. 31-52. *In* Induced mutants for cereal grain protein improvement. Proc. Res. Coord. Meet., Nicosia, Cyprus. 21–25 Apr. 1980. IAEA, Vienna. TECDOC-259.

----, and ----. 1984. Wheat and triticale breeding using gamma-ray-induced variability:

Progress report. p. 3–16. *In* Cereal grain protein improvement. Proc. of Final Res. Coord. Meet. for Cereal Grain Protein Improvement, Vienna, Austria. 6–10 Dec. 1982. IAEA, Vienna. STI/PUB/664.

Pasquini, M. 1980. Disease resistance in wheat. 2. Behavior of *Aegilops* species with respect to *Puccinia recondita* f. sp. *tritici*, *P. gaminis* f. sp. *tritici* and *Erysiphe graminis* f. sp. tritici. Genet. Agrar. 34:133–148.

Pental, D., and J.E. Gunckel. 1980. Induction and differentiation of haploid *Triticum aestivum* cv. Chinese Spring callus initiated from haploid embryos. Can. J. Bot. 58:741–744.

Pepe, J.F., and R.E. Heiner. 1975. Influence of two different dwarfing sources on yield and protein percentage in semidwarf wheat. Crop Sci. 15:637–639.

Percival, J. 1921. The wheat plant—A monograph. Duckworth and Co., London.

Peto, F.H., and J.W. Boyes. 1940. Hybridization of *Triticum* and *Agropyron*. VI. Induced fertility in vernal emmer × *A. glaucum*. Can. J. Res. 18:230–239.

Piexoto-Gomes, E., and J. Carlos-Ignaczak. 1982. IAS 63. Mutat. Breed. Newsl. 19:18.

Pink, D.A., F.G.A. Bennett, C.E. Caten, and C.N. Law. 1983. Correlated effects of homoeologous group 5 chromosomes upon infection of wheat by yellow rust and powdery mildew. Z. Pflanzenzuecht. 91:278–294.

Quinones, M.A., E.N. Larter, and D.J. Samborski. 1972. The inheritance of resistance to *Puccinia recondita* in hexaploid triticale. Can. J. Genet. Cytol. 14:495–505.

Rai, S.N., and A.C. Gaur. 1983. Nitrogen fixation by *Azospirillum* spp. and effect of *Azospirillum lipoferum* on the yield and N-uptake of wheat crop. Plant Soil 69:233–238.

Rajaram, S., B. Skovmand, H.J. Dubin, E. Torres, R.G. Anderson, A.P. Roelfs, D.J. Samborski, and I.A. Watson. 1979. Diversity of rust resistance of the CIMMYT multiline composite, its yield potential and utilization. Indian J. Genet. Plant Breed. 39:60–71.

Ramage, R.T. 1977. Varietal improvement of wheat through male sterile facilitated recurrent selection. Food Fert. Technol. Cent. Tech. Bull. 37:1–6.

Rao, M.V., S.M.A. Naqui, and J.K. Luthra. 1981. MLKS-11-a wheat multiline variety for the northeern and western plains of India. p. 7–9. *In* Indian multilines. CIMMYT, Mexico.

Rennie, R.J., and R.I. Larson. 1979. Nitrogen fixation associated with disomic chromosome substitution lines of spring wheat. Can. J. Bot. 57:2771–2775.

Riley, R. 1958. Chromosome pairing and haploids in wheat. *In* Proc. 10th Int. Congr. Genet, Vol. 2, 234–235, Montreal, 20–27 August 1958. University of Toronto Press.

----. 1966. Cytogenetics and wheat breeding. Contemp. Agric. 11–12:107–117.

----, V. Chapman, and R. Johnson. 1968. The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis. Genet. Res. 12:199–219.

----, and G. Kimber. 1966. The transfer of alien genetic variation to wheat. p. 6–36. *In* Rep. Plant Breed. Inst., Cambridge, 1964–65.

Rosichan, J.L., and R.A. Nilan. 1979. Intragenic recombination at the waxy locus in *Hordeum vulgare*. Barley Genet. Newsl. 9:79–85.

Rowell, P.L., and D.G. Miller. 1971. Induction of male sterility in wheat with 2-chloroethylphosphonic acid (Ethrel). Crop Sci. 11:629–631.

----, and ----. 1974. Effect of 2-chloroethylphosphonic acid (ethephon) on female fertility of two wheat varieties. Crop Sci. 14:31–34.

Sage, G.C.M. 1976. Nucleo-cytoplasmic relationships in wheat. Adv. Agron. 28:265–298.

Salman, R.M., R.G. Sears, and A.C. Guenzi. 1984. Genetic control of tissue culture response in winter wheat. Agron. Abstr. American Society of Agronomy, Madison, WI, p. 86.

Sando, W.J. 1935. Hybrids of wheat, rye and *Haynaldia*. J. Hered. 26:229–232.

Sarvella, P., R.A. Nilan, and C.F. Konzak. 1962. Relation of embryo structure, node position, tillering and depth of planting to the effects of X-rays in barley. Radiat. Bot. 2:89–108.

Sasakuma, T., S.S. Maan, and N.D. Williams. 1978. EMS-induced male sterility in euplasmic and alloplasmic common wheat. Crop Sci. 18:850–853.

Sato, M., and H. Gaul. 1967. Effect of ethyl methanesulfonate on the fertility of barley. Radiat. Bot. 7:7–15.

Scarascia-Mugnozza, G. 1968. Due linee di frumento duro ottenute per mutazione radioindotta. (In Italian.) Notiziario CNEN 4:3–8.

----, G.T., D. Bagnara, and A. Bozzini, 1972. Mutagenesis applied to *durum* wheat: Results and perspectives. p. 183–198. *In* Induced mutations and plant improvement. Proc. of Latin American Study Group Meet. on Induced Mutations and Plant Improvement, Buenos Aires. 16–20 Nov. 1979. IAEA, Vienna. STI/PUB/297.

Schaeffer, G.W., P.S. Baenziger, and J. Worley. 1979. Haploid plant development from anthers and *in vitro* embryo culture of wheat. Crop Sci. 19:697–702.

Schmidt, J.W., V.A. Johnson, and S.S. Maan. 1962. Hybrid wheat. Nebraska Exp. Stn. Q. 9:9.

Sears, E.R. 1941a. Amphidiploids of the seven-chromosome Triticinae. MO. Agric. Exp:. Stn. Res. Bull. 336.

----. 1941b. Chromosome pairing and fertility in hybrids and amphidiploids in the Triticinae. Mo. Agric. Exp. Stn. Res. Bull. 337.

----. 1948. The cytology and genetics of the wheats and their relatives. p. 239–270. *In* Advances in genetics II. Academic Press, New York.

----. 1956a. The systematics, cytology, and genetics of wheat. Handb. Pflanzenzuecht. II:164–187.

----. 1956b. The transfer of leaf-rust resistance from *Aegilops umbellulata* to wheat. Brookhaven Symp. Biol. 9:1–21.

----. 1966. Nullisomic-tetrasomic combinations in wheat. p. 29–45. *In* R. Riley and K.R. Lewis (ed.) Chromosome manipulation and plant genetics. Oliver and Boyd, Edinburgh, Scotland.

----. 1972. Chromosome engineering in wheat. Stadler Genet. Symp. 4:23–38.

----. 1973. *Agropyron*-wheat transfers induced by homoeologous pairing. p. 191–199. *In* 4th Int. Wheat Genet. Symp., Univ. of Missouri, Columbia.

----. 1977. An induced mutant with homoeologous pairing in wheat. Can. J. Genet. Cytol. 19:585–593.

----. 1981. Transfer of alien genetic material to wheat. p. 75–89. *In* L.T. Evans and W.J. Peacock (ed.) Wheat science today and tomorrow. Cambridge University Press, Cambridge.

----. 1982. A wheat mutation conditioning an intermediate level of homoeologous chromosome pairing. Can. J. Genet. Cytol. 24:715–719.

----. 1984. Mutations in wheat that raise the level of meiotic chromosome pairing. p. 295–300. *In* J.P. Gustafson (ed.) Gene manipulation in plant improvement. 16th Stadler Genet. Symp., Plenum Press, New York.

Sears, R.G., and E.L. Deckard. 1982. Tissue culture variability in wheat: Callus induction and plant regeneration. Crop Sci. 22:546–550.

Seitzer, J.F., and L.E. Evans. 1978. Yield gains in wheat by the pedigree method of selection and two early yield tests. Z. Pflanzenzuecht. 80:1–10.

Sharma, H.C., and B.S. Gill. 1983a. New hybrids between *Agropyron* and wheat. 2. Production, morphology, and cytogenetic analysis of F_1 hybrids and backcross derivatives. Theor. Appl. Genet. 66:111–121.

----, and ----. 1983b. Current status of wide hybridization in wheat. Euphytica 32:17–31.

----. J.G. Waines, and K.W. Foster. 1981. Variability in primitive and wild wheats for useful genetic characters. Crop Sci. 21:555–559.

Sharma-Rao, H.K. and E.R. Sears. 1964. Chemical mutagenesis in *Triticum aestivum*. Mutat. Res. 1:387–399.

Shebeski, L.H. 1967. Wheat and breeding. p. 249–272. *In* K.F. Nielsen (ed.). Proc. Can. Centennial Wheat Symp. Modern Press, Saskatoon, Sask.

Shimada, T. 1981. Haploid plants regenerated from the pollen callus of wheat (*Triticum aestivum* L.). Jpn. J. Genet. 56:581–588.

----, and T. Makino. 1975. *In vitro* culture of wheat. III. Anther culture of the A genome aneuploids in common wheat. Theor. Appl. Genet. 46:407–410.

Shkvarnikov, P.K., and M.I. Kulik. 1975. Induction of mutations in wheat. Proc. Indian Natl. Sci. Acad. 41:204–217.

Sigurbjörnsson, B. 1972. Breeding with natural and induced variability. p 3–5, 526–544. *In* Induced mutations and plant improvement. Proc. of Latin American Study Group Meet. on Induced Mutations and Plant Improvement, Buenos Aires. 16–20 Nov. 1979. IAEA, Vienna. STI/PUB/297.

Sigurbjörnsson, B., and A. Micke. 1974. Philosophy and accomplishments of mutation breeding. p. 303–343. *In* Polyploidy and induced mutations in plant breeding. Proc. Meet. on Improvement of Mutation Breeding Techniques, Bari, Italy. 2–10 Oct. 1972. IAEA, Vienna. STI/PUB/359.

Simons, M.D., J.A. Browning and K.J. Frey. 1983. Modification of tolerance of oats to crown rust induced by chemical mutagens. p. 139–150. *In* Induced mutations for disease resistance in crop plants. Vol. II. Proc. Res. Coord. Meet., Risø. 15–19 June 1981. IAEA, Vienna. STI/PUB/633.

Singh, M.P., L.S. Gupta, and H.G. Singh. 1981. Bithoor—A wheat multiline variety for Uttar Pradesh. p. 5–6. *In* Indian multilines. CIMMYT, Mexico.

Skorda, E.A. 1973. Increasing the efficiency of selection for F_2 plant yield by reducing environmental variability. p. 595–600. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO.

Smith, D.C. 1942. Intergeneric hybridization of cereals and other grasses. J. Agric. Res. 54:33–47.

----. 1943. Intergeneric hybridization of *Triticum* and other grasses, principally *Agropyron*. J. Hered. 34:219–224.

Smith, E.L., A.M. Schlehuber, H.C. Young, Jr., and L.H. Edwards. 1968. Registration of Agent wheat. Crop Sci. 8:511–512.

----, T. Tesemma, H. Pass, and G.H. Morgan. 1984. Results of 1983 wheat variety-hybrid performance test. Res. Rep. P-847, Agric. Exp. Stn., Oklahoma State Univ.

Snape, J.W. 1982. Predicting the frequencies of transgressive segregants for yield components in wheat. Theor. Appl. Genet. 62:127–134.

----, V. Chapman, J. Moss, C.E. Blanchard, and T.E. Miller. 1979. The crossabilities of wheat varieties with *Hordeum bulbosum*. Heredity 42:291–298.

----, and T.J. Riggs. 1975. Genetical consequences of single seed descent in the breeding of self-pollinating crops. Heredity 34:211–219.

Sneep,. J. 1977. Selection for yield in early generations of self-fertilizing crops. Euphytica 26:27–30.

Solari, R., and E.A. Favret. 1968. Genetic control of protein constitution in wheat endosperm and its implication on induced mutagenesis. p. 219–231. *In* Mutations in plant breeding II. Proc. of Res. Coord. Meet. on the Use of Induced Mutations in Plant Breeding, Vienna, Austria. 11–15 Sep. 1967. IAEA, Vienna. STI/PUB/182.

Sorrells, M.E., and S.E. Fritz. 1982. Application of a dominant male-sterile allele to the improvement of self-pollinated crops. Crop Sci. 22:1033–1035.

Sprague, R. 1936. Relative susceptibility of certain species of Gramineae to *Cercosporella herpotrichoides*. J. Agric. Res. 53:659–670.

Sunderland, N., and M. Roberts. 1977. New approach to pollen culture. Nature (London) 270:236–238.

Sutka, J., and G. Kovács. 1987. Chromosomal location of dwarfing gene Rht12 in wheat. Euphytica. In press.

Symes, J.R. 1972. Single plant characters as a measure of field plot performance of wheat cultivars. Aust. J. Agric. Res. 23:753–760.

Tallberg, A. 1982. Characterization of high-lysine barley genotypes. Hereditas 96:229–245.

Tanner, D.G. and D.E. Falk. 1981. The interaction of genetically controlled crossability in wheat and rye. Can. J. Genet. Cytol. 23:27–32.

Tanner, J.W., C.J. Gardener, N.C. Stoskopf, and E. Reinbergs. 1966. Some observations on upright-leaf-type small grains. Can. J. Plant Sci. 46:690.

Tavil, M.W. 1981. Mutations in wheat induced by MNH and sodium azide and combined action of them. (Russian with English summary). Cytol. Genet. 4:53–59.

Taylor, J.W., and K.S. Quisenberry. 1935. Inheritance of rye crossability in wheat hybrids. J. Am. Soc. Agric. 27:149–153.

Tee, T.S., and C.O. Qualset. 1975. Bulk populations in wheat breeding: comparison of single seed descent and random bulk methods. Euphytica 24:393–405.

Thakare, R.B., and C.O. Qualset. 1978. Empirical evaluation of single-plant and family selection strategies in wheat. Crop Sci. 18:115–118.

Thomas, J.B., P.J. Kaltsikes, and R.G. Anderson. 1981. Relation between wheat-rye crossability and seed set of common wheat after pollination with other species in the *Hordeae*. Euphytica 30:121–127.

Toda, M., T. Nakada, S. Miki, and T. Taukuda. 1972. Studies on mutation breeding in barley and wheat plants. II. Breeding of a new variety and desirable short culm strains in wheat by gamma ray irradiations. Jpn. J. Breed. 22:239–245.

Tschermak, S.E. 1930. New observations of the fertile species hybrid *Triticum turgido-villosum*. Ber. Deuts. Bot. Ges. 48:400–407. (Plant Breed. Abstr. 1:320).

Tsitsin, N.V. 1933. The *Triticum-Agropyron* hybrids. Lenin Acad. Agric. Sci., Siberian Inst. Grain Cult., Omsk. 101 (quoted by T.M. Armstrong, 1945. Emp. J. Exp. Agric. 13:41–53, and by E.R. Sears, 1948; Plant Breed. Abstr. 5:78).

———. 1936. The problem of perennial wheat. Sel. Semenovod. (Plant Breeding and Seed Production) 2:21–27. (Herbage Abstr. 7:14–15).

Tsujimoto, H., and K. Tsunewaki. 1984. Gametocidal genes in wheat and its relatives. I. Genetic analysis in common wheat of a gametocidal gene derived from *Aegilops speltoides*. Can. J. Genet. Cytol. 26:78–84.

Tsunewaki, K., T.R. Endo, and Y. Mukai. 1974. Further discovery of alien cytoplasms inducing haploids and twins in common wheat. Theor. Appl. Genet. 45:104–109.

———, Y. Mukai, T.R. Endo, S. Tsuji, and M. Murata. 1976., Genetic diversity of the cytoplasm in *Triticum and Aegilops*. VI. Distribution of the haploid-inducing cytoplasm. Jpn. J. Genet. 51:193–200.

———, Y. Mukai, and T. Ryu Endo. 1980. Detailed study of alloplasmic wheats produced at Kyoto University. p. 49–101. *In* K. Tsunewaki (ed.) Genetic diversity of the cytoplasm in *Triticum* and *Aegilops*. Japan Soc. for the Promotion of Sci. Tokyo, Japan.

Vallega, J. 1974. Historical perspective of wheat breeding in Italy. p. 115–126. *In* Proc. of 4th FAO/Rockefeller Foundation Wheat Seminar, Tehran, Iran. 21 May–2 June 1973. FAO, Rome, Italy.

Vallega, V. 1978. Search for useful genetic characters in diploid *Triticum* spp. p. 156–162. *In* S. Ramanujam (ed.) 5th Int. Wheat Genet. Symp. Indian Society of Genetics and Breeding, New Delhi, India.

Vasil, I.K. 1983. Regeneration of plants from single cells of cereals and grasses. p. 233–252. *In* P.F. Lurquin and A. Kleinhofs (ed.) Genetic engineering in eukaryotes. Plenum Press, New York.

Vavilov, N.I. 1926. Studies on the origins of cultivated plants. Bull. Appl. Bot. Plant Breed. 16:1–245.

Veruschkine, S.M. 1936. The prospects of hybridizing wheat with *Agropyron*. Sel. Semonovod. (Plant Breeding and Seed Production) 2:28–33. (Pl. Breed., Abstr. 7:595).

Viglasi, P. 1968. Short-strawed mutants of Karcag 522 winter wheat induced by gamma rays. Acta Agron. Acad. Sci. Hung. 17:205–214.

Virmani, S.S., and I.B. Edwards. 1983. Current status and future prospects for breeding hybrid rice and wheat. Adv. Agron. 36:145–213.

Wagner, J.H., M.M. Nawar, C.F. Konzak, and R.A. Nilan. 1968. The influence of pH on the biological changes induced by ethyleneimine in barley. Mutat. Res. 5:57–64.

Wall, A.M., R. Riley, and V. Chapman. 1971. Wheat mutants permitting homoeologous, meiotic chromosome pairing. Genet. Res. 18:311–328.

Walter, T.L. 1983. Kansas performance tests with winter wheat varieties. Kansas Agric. Exp. Stn., Prog. Rep. 439.

Wang, P., Y. Chen, W. Tsai, C. Wu, and S. Han. 1978. Effects of various materials and physiological conditions on induction frequency of pollen plants in winter wheat. p. 219–221. *In* H. Hu et al. (ed.) Proc. Symp. Anther Culture. Science Press, Peking.

Wei, Z.M. 1982. Pollen callus culture in *Triticum aestivum*. Theor. Appl. Genet. 63:71–73.

Wettstein-Knowles, P. von. 1979. Genetics and biosynthesis of plant epicuticular waxes. p. 1–26. *In* L.A. Appleqvist and C. Liljenberg (ed.) Advances in the biochemistry and physiology of plant lipids. Elsevier/North Holland Biomedical Press, Amsterdam.

----, P. von, and B. Søgaard. 1980. The *cer*-cqu region in barley: Gene cluster or multifunctional gene? Carlsberg Res. Commun. 45:125–141.

Whelan, E.D.P., T.G. Atkinson, and R.I. Larson. 1983. Registration of LRS-1F193 wheat germplasm. Crop Sci. 23:194.

White, W.J. 1940. Intergeneric crosses between *Triticum* and *Agropyron*. Sci. Agric. 21:198–232.

Wilson, J.A. 1962. DeKalb Agric. Assoc., Inc. contribution. Annu. Wheat News. 9:29–30.

----. 1984. Hybrid wheat breeding and commercial seed development. Plant Breed. Rev. 2:303–319.

----. and W.M. Ross. 1962. Male sterility interaction of *Triticum aestivum* and *Triticum timopheevi* cytoplasm. Wheat Inf. Serv. 14:29–31.

----, J.A. Wilson, and H.J. Schmidt. 1980. Full-dwarf × semi-dwarf hybrid wheats. p. 210–214. Proc. 3rd Int. Wheat Conf., Madrid, Spain.

Wilson, P., and C.J. Driscoll. 1983. Hybrid wheat. p. 94–23. *In* R. Frankel (ed.) Heterosis: reappraisal of theory and practice. Springer-Verlag, Berlin.

Wolfe, M.S., J.A. Barrett, and J.E.E. Jenkins. 1981. The use of cultivar mixtures for disease control. p. 73–80. *In* J.F. Jenkin and R.T. Plumb (ed.) Strategies for the control of cereal diseases. Blackwell, London.

Woloschuk, C.M., and A. McHughen. 1984. Variant wheat regenerants. IAPTC (Canada) 1st Plant Genetic Engineering Workshop. Saskatoon, Sask., Canada. (Abstr.).

Yamagata, H. 1981. Fruits and perspectives of mutation breeding. p. 11–40. *In* Progress in mutation breeding. 20th Gamma Field Symposium, Ohimaya, Ibaraki, Japan. 16–17 July.

Yamashita, K. 1968. Recommendations to stress the urgency of gene exploration and preservation in wheat and its relatives. p. 465–467. *In* K.W. Finlay and K.W. Shepherd (ed.) Proc. 3rd Int. Wheat Genet. Symp., Aust. Acad. Sci., Canberra, Australia.

Yang, H.Y., and J. Zhou. 1982. *In vitro* induction of haploid plants from unpollinated ovaries and ovules. Theor. Appl. Genet. 63:97–104.

Yonezawa, K. 1975. Method and efficiency of mutation breeding for quantitative characters. p. 39–58. 14th Gamma Field Symposium, Ohimaya, Ibaraki, Japan. 24–25 July.

----, and H. Yamagata. 1977. On the optimum mutation rate and optimum dose for practical mutation breeding. Euphytica 26:413–426.

Yoshida, S. 1972. Physiological aspects of grain yield. Annu. Rev. Plant Physiol. 23:437–464.

Zeller, F.J. 1973. 1B/1R wheat-rye chromosome substitutions and translocations. p. 209–221. *In* Proc. 4th Int. Wheat Genet. Symp., Columbia, Missouri.

----. 1981. Identification of a 4A/7R and a 7B/4R wheat-rye chromosome translocation. Theor. Appl. Genet. 59:33–37.

Zeng, J. 1983. Application of anther culture technique to crop improvement in China. p. 351–364. *In* S.K. Sen and K.L. Giles (ed.) Plant cell culture in crop improvement. Plenum Press, New York.

Zenkteller, M., and J. Straub. 1979. Cytoembryological studies on the process of fertilization and the development of haploid embryos of *Triticum aestivum* (2n=42) after crossing with *Hordeum bulbosum* (2n=14). Z. Pflanzenzuecht. 82:36–44.

Zeven, A.C. 1984. The isogenicity of near-isogenic lines of wheat. p. 103–114. *In* Vortrage

für Pflanzenzüchtung-Arbeitsgemeinschaft Pflanzenzüchtung. Gesellschaft für Pflanzenbauwissenschaften. Saatgut-Treuhandverwaltungs, Bonn, West Germany. (English.)

----, D.R. Knott, and R. Johnson. 1983. Investigation of linkage drag in near isogenic lines of wheat by testing for seedling reaction to races of stem rust, leaf rust and yellow rust. Euphytica 32:319–327.

Zhou, J. 1980. Pollen dimorphism and its relation to the formation of pollen embryos in anther culture of wheat (*Triticum aestivum*). (English Transl.)Acta Bot. Sin. 22:117–121.

Zhu, Z.C., H.S. Wu, W.K. An, and Z.Y. Liu. 1981. Induction of haploid plantlets from unpollinated ovaries of *Triticum aestivum* cultured *in vitro*. Acta Genet. Sin. 8:386–390.

Zohary, D., J.R. Harlan, and A. Vardi. 1969. The wild diploid progenitors of wheat and their breeding value. Euphytica 18:58–65.

8 Wheat Diseases

Gregory Shaner

A. Diseases of Roots, Crowns, and Lower Stems
W. W. Bockus

B. Bacterial and Fungal Blights of the Foliage and Heads of Wheat
Barry M. Cunfer

C. Rusts, Smuts, and Powdery Mildew
John F. Schafer

D. Virus Diseases of Wheat
M. K. Brakke

8 Wheat Diseases

Gregory Shaner, ***coordinator***

Diseases have been a major production hazard for wheat (*Triticum aestivum* L.) em. Thell) throughout history. Many of the landmark discoveries in plant pathology, genetics, and breeding came out of work on wheat diseases, as investigators attempted to protect this vital crop from the ravages of disease.

The scientific work directed to the control of wheat diseases has had tremendous economic impact on productivity of the crop, both on the level and stability of yield and on quality. Diseases that were formerly devastating now have been brought under satisfactory control in many parts of the world. Nonetheless, there is still much that can be done to reduce the effects of disease on the crop. As old diseases have been controlled, new diseases have sometimes appeared. Control of one disease may make available a food base for a pathogen that previously was not competitive. There is also the persistent problem of genetic variability of many pathogens of wheat, and the consequent loss of effective genetic resistance when new virulent races evolve. Some diseases may have become more serious in recent years because of changes in production practices. Cropping of wheat more frequently in a rotation, higher rates of fertilizer, minimum tillage, and irrigation all have had an effect on disease.

Control of wheat disease, whether by host plant resistance, cultural practices, or the use of pesticides, depends first on accurate diagnosis. For this reason, all of the sections in this chapter include information on symptoms and signs that are diagnostic of each disease. Information is also provided on the epidemiology of each disease, including how the pathogen survives between wheat crops, how it is spread, and how environmental conditions affect development of disease in the crop. Finally, information is provided on control.

The chapter is organized around major groups of pathogens or disease types. First, diseases of roots and lower stems are discussed. Although several taxonomically diverse pathogens are responsible for these diseases, they have many common features epidemiologically. Control measures are similar for many of these diseases.

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Next covered are the diseases of foliage or heads that are caused by a diverse group of fungi and bacteria. Many of these diseases were of relatively minor importance until the rusts and powdery mildew (*Erysiphe graminis* DC.) were brought under control. Diseases caused by the highly specialized fungal parasites (rusts, powdery mildew, and smuts) are covered next. These diseases share many common features with respect to control.

Finally, diseases caused by viruses are dealt with. The uniqueness of viruses as pathogens makes this a logical grouping. With improvement in diagnostic techniques, we are now realizing the economic importance of these diseases.

8A Diseases of Roots, Crowns, and Lower Stems

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The root system, crown, and lower stems of a wheat plant are unique habitats for microorganisms attacking those organs, unique because the pathogens complete at least part of their life cycle in intimate contact with the soil. Various components of the soil environment have significant effects on the longevity and activity of soilborne wheat pathogens and often determine where and when severe disease outbreaks occur.

The soil environment can be divided into a physicochemical and a biological component. Although rapid changes in the physicochemical component can occur (e.g., soil moisture during a rain) the soil environment is generally more buffered than the aerial environment, with such factors as soil texture, clay content, and bulk pH remaining relatively constant. Nevertheless, the physical and chemical makeup of a soil has a profound effect upon the pathogens themselves, the wheat plant, and the nonpathogenic resident soil microflora (Baker and Snyder, 1965; Bruehl, 1975). Many of the control measures to reduce soilborne wheat diseases involve manipulation of certain physicochemical parameters of the soil.

Interactions among soil physical and chemical factors are complex, and the inclusion of the diverse biological community produces an extremely complex environment (Griffin, 1972). Although various types of worms, saprophytic nematodes, insects, protozoa, and plant parts occur in wheat field soil, it is the resident bacteria, Actinomycetes, fungi, and wheat plants themselves that most influence the activity of wheat pathogens (Cook and Baker, 1983). Many control recommendations (e.g., tillage and crop rotation) for diseases of roots, crowns, and lower stems are effective either directly or indirectly as a result of the activity of the resident microflora.

The wheat pathogens discussed in this section cause the following

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diseases: common root and crown rot, Pythium root rot, take-all, Rhizoctonia root rot and sharp eyespot, strawbreaker foot rot, and Cephalosporium stripe. Root-lesion nematodes and stubby-root nematodes are also discussed. These pathogens may be divided into two groups: those that can persist in soil for many years in the absence of a susceptible wheat crop (*soil inhabitants*) and those that cannot (*soil invaders*). Members of the first group include those that cause the diseases Rhizoctonia root rot, Pythium root rot, common root and crown rot, as well as root-lesion nematodes and stubby-root nematodes. They tend to be ubiquitous and are virtually unavoidable. With a conducive environment and a susceptible host, severe losses can occur. These pathogens survive in the absence of wheat, either by saprophytic growth on materials available in the soil or by virtue of an extremely broad host range. Most of the controls for this group involve manipulating the environment in which wheat is grown. Pathogens that do not survive well in soil in the absence of wheat include those that cause take-all, strawbreaker foot rot, and Cephalosporium stripe. They are introduced into a wheat production field from elsewhere. They may come from other crops or weed hosts or from nearby wheat fields and are usually dispersed by wind, farm machinery, or living organisms. Once introduced into a field they multiply on the wheat crop, and their populations increase, particularly when wheat is continuously cropped in the same field. However, since they are not competitive with the resident soil microflora, their populations decrease in the absence of a susceptible crop. Thus, these pathogens are characterized by an increasing parasitic phase while wheat is growing and a relatively rapid declining saprophytic phase when wheat is absent. These soilborne pathogens survive between wheat crops in one of two ways. They either produce dormant structures (e.g., spores and mycelium) or, for some limited period, saprophytically possess wheat residue that they have colonized during their parasitic phase.

The diseases in this section can be characterized further by their epidemiology. Some, such as take-all and Cephalosporium stripe, produce inoculum only once a year, and the amount produced is correlated with the amount of infection during the previous wheat cropping season. The potential for a given level of inoculum to cause disease in a subsequent crop is influenced by the interval between crops, and the environment. However, with these diseases, if there is only a small amount of inoculum in a field, little yield loss will result even when a susceptible crop is grown under an environment conducive to disease development. Although the fungi causing Rhizoctonia root rot, sharp eyespot, and common root and crown rot and the root-lesion nematodes are soil inhabitants and can produce inoculum several times during a season, they best fit with this group (soil invaders) epidemiologically. The soil population of these pathogens before seeding may largely determine the amount of damage that can occur in a given year, since they produce secondary inoculum more slowly.

Differing from the above group are the pathogens that cause Pythium root rot and strawbreaker foot rot, and the stubby root nematode, all of which can produce large amounts of inoculum more than once during the growing season. Inoculum which initially infects a wheat crop can produce more inoculum that is able to cause additional infections on the same crop, and this in turn may produce even more inoculum. Thus, even a relatively small amount of inoculum initially present in a field can cause considerable losses if a susceptible crop is grown under an environment favorable to disease. None of these three pathogens, however, produce secondary inoculum as explosively as many foliar pathogens.

8A–1 SELECTED DISEASES OF ROOTS, CROWNS, AND LOWER STEMS

There are several publications that deal with wheat disease diagnosis (Bruehl, 1967; Butler, 1961; Dickson, 1956; Sallans, 1965; Sprague, 1950; Wiese, 1987; Zillinsky, 1983) and no attempt will be made here to construct a diagnostic key for diseases of roots, crowns, and lower stems. These publications also cover the taxonomy of the pathogens. Several of the more important diseases of wheat in North America will be covered in this section, but this is not intended to be a complete list. The major symptoms of these diseases are described here with emphasis on characteristic signs and/or symptoms of each pathogen. These diseases can all occur by themselves; however, combinations of pathogens may cause some disease situations. Following the description of symptoms for each disease is a discussion of the causal agents and disease cycle.

8A–1.1 Common Root and Crown Rot

Symptoms of common root and crown rot can occur early in the cropping season. Plants may be unthrifty, die after emergence, or even fail to emerge. Plants with common root and crown rot are also more susceptible to winter-kill, and this may result in patches of winter wheat which fail to regrow in the spring (Fenster et al., 1972). Plants in these vegetative stages of growth display elongated brown-to-black necrotic lesions 0.1 to 2.5 cm in length on roots, crowns, and subcrown internodes (Plates 8A–1 and 8A–2). Plants which have been killed usually have a brown rooted internal crown area.

More mature plants also are affected by common root and crown rot, with symptoms often becoming more obvious after heading. Above ground symptoms are stunting, poor tillering, chlorosis, premature death of tillers (whiteheads), and shriveled grain. Affected plants may occur scattered across the field or, more commonly, in definite patches. As with diseased seedlings, mature plants show a discolored rotted internal crown area (Plate 8A–3) and may have a chocolate brown discoloration of the lower

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Chapter 8—Wheat Diseases

Section 8A: Diseases of Roots, Crowns, and Lower Stems

W. W. Bockus

Plates 8A-1, 8A-2, 8A-3, 8A-4, 8A-5, 8A-6, 8A-7, 8A-8, 8A-9, 8A-10, 8A-11, 8A-12, and 8A-13

Chapter 9—Insect and Mite Pests of Wheat

J. H. Hatchett, K. J. Starks, and J. A. Webster

Plates 9-1 and 9-2

Plate 8A–1. Subcrown internode and roots of wheat seedlings with dark, necrotic lesions caused by one of the common root and crown rot fungi, *Bipolaris sorokiniana*.

Plate 8A–2. Close-up of subcrown internode lesions caused by *Bipolaris sorokiniana*, showing spores produced by the fungus.

Plate 8A–3. Brown, rotten internal crown area of headed wheat plant with common root and crown rot. (Photo by W.G. Willis.)

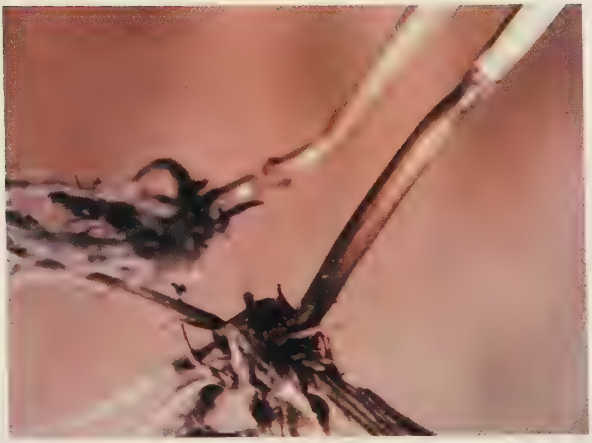

Plate 8A–4. Brown discoloration of foot area, caused by *Fusarium roseum*.

Plate 8A–5. *Right*: Root system stunted by Pythium root rot. *Left*: Healthy root system.

Plate 8A–6. Patches of prematurely ripe tillers (whiteheads) caused by take-all.

Plate 8A–7. Wheat plant affected by take-all, with leaf sheaths stripped away showing black discoloration of culm base. (Photo by W.G. Willis.)

Plate 8A–8. Wheat roots with take-all lesions, showing dark runner hyphae of *Gaeumannomyces graminis* var. *tritici*.

Plate 8A–9. Wheat culm bases with sharp eyespot lesions caused by *Rhizoctonia cerealis*. (Photo by P.E. Lipps.)

Plate 8A–10. Strawbreaker foot rot lesion on wheat culm base showing black pseudoparenchyma (center) of the fungus *Pseudocercosporella herpotrichoides* and indistinct lesions margins. (Photo by T.D. Murray.)

Plate 8A–11. Winter wheat at the jointing growth stage showing yellow leaf stripes on lower leaves indicative of Cephalosporium stripe.

Plate 8A–12. Close-up of winter wheat tiller with Cephalosporium stripe, showing two stripes on leaf blade and sheath and dark vascular bundles associated with the stripes.

Plate 8A–13. *Left*: Prematurely ripe tillers (whiteheads) of winter wheat caused by Cephalosporium stripe. *Right*: Healthy wheat. (Photo by W.G. Willis.)

Plate 9–1. Greenbug colony on wheat leaf.

Plate 9–2. Wheat damaged by greenbug.

internodes of the culm (Plate 8A–4). The brown crown and lower internode associated with common root and crown rot helps differentiate it from the black discoloration seen with take-all. Isolation of the causal organism will confirm the diagnosis.

8A-1.1.1 Causal Agents and Disease Cycle

Several distinctly different fungi can cause this disease singly or in combination. Usually only one of the common root and crown rot fungi predominates in a given wheat-growing area, and thus a somewhat different disease situation is likely to exist in another location, where a different fungus or combination of fungi predominates. One locale may have one or more of the following manifestations of common root and crown rot: seedling blight, root rot, subcrown internode rot, crown rot, or foot rot. Each situation is unique and may require a different control program.

The fungi associated with common root and crown rot are: *Bipolaris sorokiniana* (Sacc. in Sorok.) Shoem., which is particularly important in Canada and the north-central USA (Ledingham et al., 1972); *Fusarium roseum* Link emend. Snyd. and Hans. 'Culmorum' and *F. roseum* 'Graminearum' important in the Pacific Northwest (Cook, 1980); and a combination of *B. sorokiniana* and several *Fusarium* spp., including *F. roseum* 'Acuminatum', *F. roseum* 'Avenaceum' and *F. roseum* 'Culmorum' in the Great Plains (Hill et al., 1983; Watkins et al., 1980). The importance of a fungus in a given area appears to be determined by environment, since low populations of all the fungi probably occur wherever wheat is grown (Hill et al., 1983; Wiese, 1987). Yield losses from these problems have been reported to average from 5 to 7% in Canada and as high as 1000 kg ha^{-1} in affected fields in the Pacific Northwest (Cook, 1980).

Many environmental factors affect common root and crown rot development. Wet soil is needed for initial fungal infection of seedling roots, subcrown internodes, and crowns. If wet conditions persist and soil temperatures are not optimal for seedling establishment, seedling blight may occur. After infection, plant stress plays a significant role in the amount of damage that results. Moisture stress, winds, and lack of snow cover reduce vigor and survival of infected winter wheat seedlings (Fenster et al., 1972). Moisture stress also plays a most important role in premature death of affected plants after heading. Any cultural practice that favors soil moisture loss (e.g., early seeding of winter wheat, over-fertilization, high plant populations, weeds), will enhance the effects of the disease.

Spores of *B. sorokiniana* and *Fusarium* spp. can persist in soil for years (Diehl et al., 1982; Sitton and Cook, 1981) and are found in virtually all wheat-growing areas. These fungi have a broad range of hosts upon which they can increase their population of spores or mycelial inoculum. Thus, contact of wheat with the common root and crown rot fungi is unavoidable, even in fields that have not been cropped to wheat for several years. Continuous cropping of susceptible hosts can, however,

result in extremely high pathogen populations with a concomitant increase in the potential for severe yield loss (Diehl et al., 1982). With an environment conducive for disease even relatively small soil populations can cause significant losses.

Soilborne *B. sorokiniana* spores or mycelium from infested debris cause discrete lesions on roots, subcrown internodes, and crowns. The more inoculum in the soil, the higher the number of lesions. Infections from *Fusarium* spp. arising from soilborne spores or mycelium tend to infect emerging crown roots or openings around crown roots (Cook, 1980). Infections by *B. sorokiniana* do not tend to move laterally. In contrast, under dry conditions after heading, *Fusarium* spp. can move from the crown up several internodes above the soil line. All of the common root and crown rot fungi can sporulate on infected host debris and, after harvest, the spores and debris are incorporated into the soil by tillage.

8A–1.2 Pythium Root Rot

Pythium spp. can infect below-ground parts of wheat throughout the season. Reduced plant populations, seedling death, stunting, yellowing, and delayed maturity are some of the more obvious symptoms caused by Pythium root rot. The milder symptoms of reduced tillering and poor plant vigor may go unnoticed. This insidious root rot phase can be difficult to detect without a comparison to adjacent, healthy wheat (Plate 8A–5).

Plants displaying more obvious symptoms generally occur in patches. Below-ground parts will have a wet, extensively rotted, brown root system. Observation of oospores in rotted tissue or isolation of *Pythium* spp. may be necessary to confirm the diagnosis. Root tips of infected plants with subtle or no above ground symptoms will be yellow to brown. Since the rot may be confined to the smallest rootlets, care must be taken in sampling and observing the roots of suspected diseased plants.

8A–1.2.1 Causal Agents and Disease Cycle

Pythium root rot, also called browning root rot, may be caused by one or more species of the soilborne fungal genus *Pythium*. These fungi are in all agricultural soils and have a wide host range, making them unavoidable pathogens. Although reduced seedling emergence and plant death can occur (Bruehl, 1967; Wiese, 1977), damage is usually due to reduced plant vigor by chronic root rot on the fine rootlets (Cook and Haglund, 1982). Reducing the overall health of the root system in this way lowers the ability of the plant to absorb and transport nutrients and water from the soil. *Pythium* is primarily confined to the seminal and crown roots, although under extremely wet conditions crown rot may develop. The disease can reduce yield by 15 to 20% and yet go largely undetected (Bruehl, 1953; Cook and Haglund, 1982). Conditions which favor the disease are moist soil (Dickson, 1956), large amounts of crop

residue in and on the soil (Cook et al., 1980), and P-deficient soil (Bruehl, 1951b).

The *Pythium* spp. considered here are soil inhabitants. They can survive as dormant oospores (thick-walled spores) in soil for at least 5 yr (Bruehl, 1953; Wiese, 1977) and can colonize soilborne crop residues to use as a food base and refuge when wheat is not present. Some species produce motile zoospores that move through water to contact roots upon which they encyst, germinate, and infect. Other species produce conidia which germinate by production of a germ tube that infects the root. Infections occurs rapidly and may be most detrimental to the fine feeder roots (Bruehl, 1953; Wilhelm, 1965). The mycelium ramifies through the root cells and later produces oospores within the infected root area. The fungus can also sporulate on infected tissue to produce additional zoospores and conidia. After host death the fungus returns to a dormant or saprophytic state until it encounters another susceptible host or wheat is again seeded.

8A–1.3 Take-all

Symptoms on winter wheat usually do not occur during the fall. Aboveground symptoms usually first appear during early spring in severely affected areas. Plants may be stunted and chlorotic, and lower leaves may die prematurely. In more mildly affected areas, aboveground symptoms may not appear until after heading, when spikes ripen prematurely, becoming whiteheads. Affected areas commonly are circular patches 1 to 10 m in diameter (Plate 8A–6), although in some cases the disease may be uniformly distributed throughout a field. Killed plants pull easily from the soil, since the root system is rotted and brittle. Positive diagnosis late in the season is made by stripping off the leaf sheaths from the basal stem area and observing the shiny black mycelial plaques of the fungus on the culm (Plate 8A–7). Diagnosis at earlier times or in mild cases can be made by digging plants, washing the soil from the roots, and observing black lesions on the roots and subcrown internode. Positive diagnosis at these times should be made by observing roots under a dissecting microscope for melanized runner hyphae on the surface of the roots (Plate 8A–8).

8A–1.3.1 Causal Agent and Disease Cycle

Take-all is a severe root and foot rot of wheat caused by the soilborne fungus *Gaeumannomyces graminis* (Sacc) von Arx & Olivier var. *tritici* Walker. The disease can occur wherever wheat is continuously cropped; severe losses have been reported from Kansas (Bockus, 1983), Oregon (Taylor et al., 1983), Washington (Cook, 1981), Arkansas (Dolezal and Jones, 1981), Indiana (Huber, 1981), and Montana (Junke et al., 1984). Winter wheat is usually damaged more than spring wheat (Wiese, 1977). Significant losses can occur with few aboveground symptoms, but when

stunting and whiteheads are evident, yields are usually reduced 50% (Slope and Cox, 1964). Moist, loose, alkaline soils, reduced tillage, early planting, continuous cropping of susceptible hosts, and poor fertility favor take-all.

Gaeumannomyces graminis var. *tritici* survives between wheat crops either parasitically on volunteer wheat or grassy weeds within or near the field or saprophytically in infested wheat residue. Infested plant material can be moved around by wind, water, animals, and farm machinery and may introduce the fungus into a field. During several years of consecutive wheat cropping the population of the fungus increases to damaging levels. If there is a high infestation of grassy weeds infected with *G. graminis* var. *tritici* in a field which is not planted to wheat, then severe take-all may occur on wheat planted in that field for the first time.

Although sexual and asexual spores of the fungus occur (Speakman, 1982; Weste and Thrower, 1963) they are probably of little consequence in the field (Walker, 1975) and it is the mycelium in infested debris that serves as the infective agent for wheat. This debris functions as a refuge and food base enabling the fungus to survive and subsequently infect the roots of wheat plants. Infections can occur at any time during the season, although it is the early fall infections on winter wheat that produce the most damage (Bockus, 1983). The fungus has an ectotrophic growth habit on colonized roots producing dark runner hyphae on the surface of the root that periodically penetrate the root to produce a lesion. In this way a single infection can progress up and down a root and onto other, nearby roots. In advanced stages of the disease the rot may progress up to and above the crown area. When this occurs the plant is usually killed. After harvest, mycelium within rotted root or crown pieces serves as the survival site for the fungus and the inoculum source for the subsequent wheat crop.

A phenomenon called *take-all decline* is associated with long-term continuous wheat production (Shipton, 1975). In fields where this occurs, *G. graminis* is biologically suppressed by antagonistic microorganisms (Shipton et al., 1973) and it may be possible in the future to suppress the disease by manipulating these organisms (Weller and Cook, 1983). Suppressive microorganisms die as quickly as the take-all fungus itself in most crop rotations, and severe take-all often develops in these fields in the 2nd and 3rd yr of continuous wheat after rotation. Therefore, in fields exhibiting take-all decline it may be best to maintain continuous wheat to keep suppressiveness at an effective level.

8A–1.4 Rhizoctonia Root Rot and Sharp Eyespot

The root rot disease is usually a problem on seedlings. Small, 1- to 3-m diameter circular patches of diseased plants occur, usually with only a few scattered patches per field. Patches may occur in the same position for several years. Larger patches or numerous coalescing ones are infrequent. The margins of the patches change sharply from diseased to healthy

areas. Plants within the patch are stunted, with rolled leaves pointing upwards. Depending on the severity of the rot, plants may recover or eventually die. Where plants recover there is a delay in maturity compared to the rest of the crop.

Roots of affected plants display a brown rot of tips and intermediate portions of the root. Tip attack can stimulate lateral root development, which gives a highly branched root system. Lateral roots are subsequently attacked also. Roots are often so severely rotted that nothing but a brown stub (*needle point*) is left. The disease may be confused with other root disorders which produce a brown discoloration, and isolation and identification of the causal fungus (*Rhizoctonia solani* Kuhn) may be necessary. Characteristic broad hyphae of *R. solani* can often be seen on roots stained with trypan blue. There is a definite pathogenic association of *R. solani* and root lesion nematodes which should be considered when diagnosing a "bare patch" problem.

The sharp eyespot symptom is caused by closely related strains of *R. solani* and *R. cerealis* VanHoeven, but it is a foot rot disease rather than a root problem. Lesions occur on lower leaf sheaths and appear lens-shaped with a sharper margin than lesions of strawbreaker foot rot (Plate 8A–9). The tan centers of the lesions are surrounded by dark brown borders. If mycelium and sclerotia occur in the center of the lesion they are easily rubbed off, in contrast to the fungus stroma in the center of strawbreaker foot rot lesions.

8A–1.4.1 Causal Agents and Disease Cycle

These two diseases have been grouped together since they are caused by morphologically similar fungi of the *Rhizoctonia* group. *Rhizoctonia solani* and *R. cerealis* have been implicated in the sharp eyespot disease and *R. solani* in the root rot disease. Isolates causing one disease apparently do not cause the other (Bruehl, 1951a; Lipps and Herr, 1982).

Rhizoctonia is a ubiquitous, soilborne fungus and is therefore present in most agricultural fields. Since it is a soil inhabitant, infections can occur whenever environmental conditions are conducive for disease (Parmeter, 1970). In North America, neither disease is considered to be of widespread economic concern, although losses can occur in isolated fields. Losses are most severe under continuous cropping regimes, on acid, sandy, dry soils, reduced tillage, and under cool temperatures (Murray, 1981; Pitt, 1964; Samuel and Garrett, 1932).

Rhizoctonia can survive in the soil between wheat crops by saprophytically utilizing soilborne debris for nutrients (Butler, 1961). It also produces sclerotia, resistant structures able to persist in a dormant state for a long time. Combined with these survival strategies is the ability to attack a wide variety of hosts (Sprague, 1950), making it difficult to avoid the fungus.

Mycelium from infested soilborne debris, growing through the soil, or from sclerotia comes into contact with a wheat plant and is capable

of directly penetrating the epidermis (Murray, 1981; Samuel and Garrett, 1932). Stem-infecting isolates penetrate via infection pegs from a cushion of hyphae formed on the host surface (Flentje, 1957; Stern and Jones, 1978). After successful entry into the host, *Rhizoctonia* ramifies the tissue and can produce sclerotia (Parmeter, 1970). After wheat harvest the parasitically colonized residue, and any accompanying sclerotia, are returned to the soil.

8A–1.5 Strawbreaker Foot Rot

Strawbreaker foot rot is a true foot rot disease since it does not affect roots and is confined to the base of the culm (the foot). Although infection of winter wheat can occur during fall and winter, symptoms are usually not apparent until spring and often after heading. The fungus produces discrete lesions which begin on the outer leaf sheath and expand laterally and internally through the leaf sheaths and eventually through the culm causing a sudden collapse of the culm in the center of the lesion. This becomes brittle and the culm easily breaks at that point. Single lesions have a characteristic elliptical "eyespot" shape although when lesions occur close together they coalesce and obliterate that effect. The margin of eyespot lesions are less distinct than for the sharp eyespot disease. A black pseudoparenchyma produced by the fungus occurs in the center of foot rot lesions and does not rub off easily (Plate 8A–10). This is highly diagnostic of the disease. When the fungus penetrates through the culm it kills it, producing a whitehead. Severely diseased culms lodge easily, breaking toward the lesion.

8A–1.5.1 Causal Agent and Disease Cycle

Pseudocercosporella herpotrichoides (Fron) Deighton forms lesions on the culm within 15 cm of the soil surface, starting on the outer leaf sheaths and penetrating through the culm. Strawbreaker is more severe on winter wheat than spring wheat and is primarily important in the Pacific Northwest and Great Lakes regions of the USA, although it has caused losses in the Great Plains also. The disease is favored by continuous cropping of susceptible hosts; cool moist weather during fall, winter, and early spring; poorly drained, heavy, fertile soils; and a dense crop canopy. Typical yield losses under these conditions in the Pacific Northwest run over 25%, although greater losses are possible (Bruehl et al., 1974).

Pseudocercosporella herpotrichoides survives between wheat plantings primarily on old infested stubble from the previous crop and can remain viable for at least 2 to 3 yr in that habitat (Macer, 1961). Although other crop and weed hosts are attacked by the fungus, infested residue within a field is the most important source of inoculum. Whenever cool moist conditions occur from fall through spring the fungus sporulates on the refuse and the spores are disseminated by splashing rain for up to

1.3 m (Rowe and Powelson, 1973a). Spore production can occur for over 3 months if weather conditions conducive to sporulation continue. Conidia contacting the lower stem area of wheat require high relative humidities to infect (Rowe and Powelson, 1973b). After infection the fungus penetrates the leaf sheath and the culm. This weakens the stem, resulting in lodging; multiple infections on a single culm girdle and kill it outright (Murray and Bruehl, 1983). Secondary conidia from lesions can be produced within 15 days after an infection (Bruehl, 1967), although inoculum from residue is most important in causing epidemics (Rowe and Powelson, 1973a). During and after harvest the residue infested with *P. herpotrichoides* is returned to the soil surface, to complete the cycle.

8A–1.6 Cephalosporium Stripe

Symptoms are observed only on winter wheat and only after growth has resumed following the winter. Yellow stripes 3 to 4 mm wide on leaves are the first symptoms of infection by *Cephalosporium gramineum* Nisikado & Ikata. There are usually one or two on the leaf although as many as four may occur. Stripes are observed on lower leaves at the beginning of jointing and will appear on successively higher leaves during jointing and heading (Plate 8A–11). Leaves with stripes rapidly become necrotic making the stripes no longer evident. Although the fungus infects through the roots, no symptoms are visible on roots. Associated with the stripes are darkened vascular bundles that run down the middle of the stripe on the leaf blade and sheath (Plate 8A–12). The dark vascular bundle passing through the nodal region of a striped leaf can be seen in a longitudinal cut through the node. These dark bundles are specifically diagnostic of Cephalosporium stripe. Infected plants are usually stunted and whiteheaded (Plate 8A–13). They are generally intermingled with taller uninfected culms, giving the field a ragged appearance. The disease may be distributed along edges of fields or low areas within a field, although usually plants in the entire field are affected. After maturity, culms below nodes are darkened on infected tillers, a symptom similar to frost injury.

8A–1.6.1 Causal Agent and Disease Cycle

Cephalosporium gramineum, the cause of Cephalosporium stripe, is the only fungal vascular pathogen of winter wheat. It is widespread in North America and causes severe losses in Kansas (Bockus and Sim, 1982; Willis and Shively, 1974), Montana (Johnston and Mathre, 1972), the Great Lakes area (Gerdeman and Wiebel, 1960; Smith et al., 1966; Tyler and Dickens, 1957; Wiese and Ravenscroft, 1975), and the Pacific Northwest (Bruehl, 1968). The disease is a problem only on winter wheat and does not infect spring wheat in the field. The disease is favored by high soil moisture during fall and winter (Bruehl, 1968) and acidic soils ($pH < 5.5$) (Bruehl and Lai, 1968), and in areas where excessive soil

movement occurs during winter freezing and thawing (Morton and Mathre, 1980). Without adequate control measures, yield losses of 50% are common in such conditions (Bockus et al., 1983; Bruehl, 1968; Johnston and Mathre, 1972) and losses of 70 to 85% have been reported (Bockus and Sim, 1982; Richardson and Rennie, 1970).

In some areas Cephalosporium stripe is severe where winter wheat is grown every other year in the crop rotation (Latin et al., 1982), while in other areas it is important only where winter wheat is continuously cropped (Bockus et al., 1983). The ability of *C. gramineum* to survive and sporulate from wheat residue in a given environment is one important factor determining how cropping sequences affect the disease (Wiese and Ravenscroft, 1975). The fungus persists between crops in residue from the previous wheat crop that was parasitically colonized and that remains on or within 8 cm of the soil surface (Wiese and Ravenscroft, 1975). When conditions are favorable during the fall and winter it sporulates from the wheat refuse, resulting in as many as 10^5 conidia per gram soil (Wiese and Ravenscroft, 1975). *Cephalosporium gramineum* is a root-infecting fungus and gains entry either by spore germination and direct penetration of the root after the root has been frozen and thawed (Bailey et al., 1982) or by passive spore uptake after root wounding caused by soil heaving (Bruehl, 1968; Morton and Mathre, 1980). After infection, the fungus systemically invades the plant during the spring by colonizing the xylem vessels and produces a toxin (Creatura et al., 1981) which may elicit the stripe symptoms on the leaves. Following harvest, the systemically colonized residue is again returned to the soil to complete the cycle.

8A–1.7 Root-lesion Nematode

As with most soilborne pathogens, root-lesion nematodes can cause both acute and chronic damage to wheat. Acute symptoms include plant death, yellowing, and stunting, and in combination with other diseases (especially Rhizoctonia root rot), can result in large diseased patches within fields (Fig. 8A–1 and 2). Less pronounced damage, such as poor tillering, may go unnoticed, although forage or grain yields may be reduced. In all cases examination of the roots for necrotic lesions, nematodes, and eggs inside roots (Fig. 8A–3) or extraction of nematodes from root tissue is necessary for diagnosis.

Root-lesion nematodes may cause no root discoloration, but where lesions occur they vary from round to elongated and from lightly discolored to dark brown. Root necrosis is a result of interactions between the feeding enzymes excreted by the nematode and host materials. However, the degree of necrosis may not be directly related to the amount of plant damage.

8A–1.7.1 Causal Agents and Disease Cycle

Root-lesion nematodes are microscopic eelworms belonging to the genus *Pratylenchus*; they occur in agricultural soils the world over (Thames,

Fig. 8A–1. Winter wheat severly stunted by a combination of root-lesion nematodes and common root and crown rot (*foreground left*). (Photo by C.C. Russell.)

Fig. 8A–2. *Right*: Winter wheat stunted by a combination of root-lesion nematodes and common root and crown rot. *Left*: Protected by a nematicide. (Photo by C.C. Russell.)

1982). In North America they may be the most important nematodes on wheat, given the absence, or minor importance, of the cyst and root-knot nematodes on wheat. Root-lesion nematodes are classified as obligate parasites, since they need a living host to complete their life cycle. The infection, reproduction, and spread of these nematodes are favored by sandy soils and warm soil temperatures (30–32° C) (Baxter and Blake,

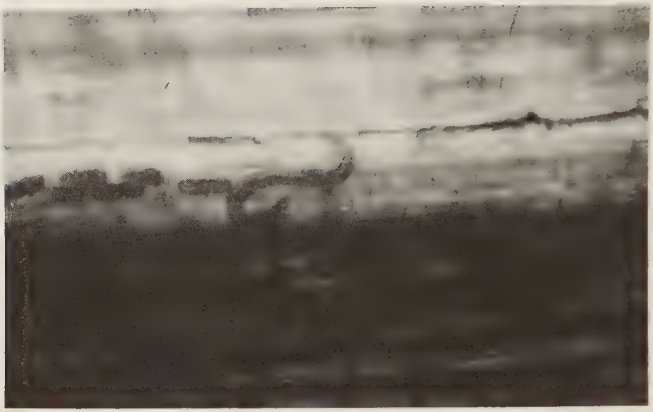

Fig. 8A–3. Wheat root with root-lesion nematode and eggs. (Photo by T.C. Todd.)

1968). Active spread within the soil is usually only about 3 cm per month (Endo, 1959).

Direct losses from root-lesion nematodes on wheat are incompletely assessed (Wiese, 1987); however, they have been implicated as an important component of root rot complexes (Benedict and Mountain, 1956; Mountain, 1954). The effect apparently involves physical disruption of the host as well as physiological stress in which hydrolytic enzymes produced by the nematode react with plant materials to produce phenolic substances (Mountain, 1965).

Under greenhouse conditions, synergism occurs between root-lesion nematodes and root rot fungi, resulting in significantly more wheat root necrosis than with nematodes or fungi alone (Todd, 1980). Thus, their interactive potential and widespread distribution should make them an important consideration when analyzing root and crown rot problems.

Lesion nematodes are migratory endoparasites; that is, they can enter and move within the root tissue as well as leave the infected root to attack other roots. They are usually confined to the epidermis and cortex and can reproduce within the root. They move from cell to cell by penetrating cell walls, and disrupt and ingest cell contents. Eggs are deposited within the root, or in the soil when female nematodes are outside the root. There are four larval stages (three outside the egg); the fourth molt produces the adult. Both larvae and adults are pathogenic and a generation is completed in 20 to 50 days when conditions are favorable for reproduction (Thames, 1982).

8A–1.8 Stubby-root Nematodes

Soil infestations of stubby-root nematodes produce stunted, spindly plants that may be easily pulled from the soil (Fig. 8A–4). The most conspicuous symptom is the cessation of root growth followed by proliferation of lateral roots that subsequently are also attacked and cease

Fig. 8A–4. Wheat plants stunted by stubby-root nematodes (foreground). (Photo by C.C. Russell.)

to elongate. This produces a highly branched, stubby root system, normally with little discoloration; this symptom is highly diagnostic of stubby-root nematode damage. The widespread distribution of these nematodes and the ability of relatively low populations to reduce plant vigor indicates that they may mildly depress yields over large acreages.

8A–1.8.1 Causal Agents and Disease Cycle

These microscopic nematodes which attack wheat belong to the genus *Paratrichodorus*, with *P. cristiei* (Allen) Sidd. probably the most important species. They are distributed worldwide and reported from many locations in the USA (Perry and Rhoades, 1982). Like the root-lesion nematodes, they are obligate parasites and have a very broad host range (Rohde and Jenkins, 1957b). Stubby-root nematodes are favored by sandy soils and warm (27° C) temperatures (Young and Struble, 1966). They can increase in number rapidly. They can also travel several cm per h in soil and transmit viruses in crops other than wheat (Jenkins and Taylor, 1967).

Paratrichodorus spp. are ectoparasites, remaining outside the root to complete their life cycle. However, during feeding at the root tip most of their bodies may be located between the root cap and root meristem (Russell and Perry, 1966). They can also feed on epidermal and root hair cells by thrusting the stylet into the cell (Russell and Perry, 1966). Excretions by the nematode probably aid in softening host cell walls to aid stylet penetration and also predigest cell cytoplasm before ingestion. The nematodes apparently extend a feeding tube through the hole made by the stylet, through which the host material is taken into the parasite's body.

Either relatively few nematodes feeding at the root apical meristem or relatively many feeding on root epidermal cells cause the stubby-root

symptom. Esophageal secretions transported to the root tip disrupt the meristematic activity of the region, and without cell division the root ceases to elongate (Rohde and Jenkins, 1957b). The plant may then produce lateral roots; if they in turn are parasitized, typical symptoms occur.

The females can lay numerous eggs in a short time in the soil. The first larval stage occurs within the egg and is released upon hatching. It passes through a second and most likely a third and fourth larval stage before adults are produced (Russell, 1962). Second stage larvae, adults, and probably all larval stages in between, attack roots in a similar manner (Russell and Perry, 1966). The entire life cycle may be completed in as few as 16 days (Rohde and Jenkins, 1957a); this with their fecundity, gives stubby-root nematodes the capacity to reach high soil populations rapidly (Perry, 1953). However, when they feed behind the root cap even low populations of these nematodes can produce the stubby-root symptom (Christie and Perry, 1951).

8A–2 CONTROL

Wheat growers are often concerned with several different diseases, and control procedures for any given disease must not be in conflict with procedures for other diseases or with standard weed control, insect control, and other agronomic practices. Economic control of diseases of roots, crowns, and lower stems of wheat usually results when several control procedures are integrated into a grower's production scheme. Discussed here are control schedules integrated into a full-cropping season, from before seeding to after harvest.

8A–2.1 Cultivar Selection

Adapted cultivars with high levels of resistance (approaching immunity) to the diseases described above are lacking. However, high-yielding cultivars with moderate resistance to some of these diseases have been developed, or resistant germplasm identified. These diseases include: take-all (Patterson et al., 1979), Cephalosporium stripe (Martin et al., 1983b; Mathre and Johnston, 1975; Morton and Mathre, 1980), strawbreaker foot rot (Murray and Bruehl, 1983), and common root and crown rot (Larson and Atkinson, 1982; Statler and Darlington, 1972). Although some of these resistances are polygenically inherited (Martin et al., 1983a; Murray and Bruehl, 1983), procedures have been established for selecting more resistant cultivars while maintaining yield. The number of resistant cultivars should increase in the future, and when combined with other controls, should greatly reduce disease loss. Resistant cultivars should be considered in areas where root, crown, and foot diseases are important.

8A–2.2 Chemical Seed Treatment

In the past, seed-treatment fungicides for wheat have primarily been used to control seedborne diseases. The currently labeled fungicides also

protect plants against the seedling blight phase of common root and crown rot; however, most will not control the disease as it occurs on more mature plants (Stack, 1982). Research has shown the potential to control other root diseases with seed treatment chemicals including take-all (Bockus, 1983), Pythium root rot (Cook et al., 1980), common root and crown rot (Chinn, 1978), and root-lesion nematode (Todd, 1980). Use of systemic materials is necessary for chemical translocation to occur from the seed to the roots, resulting in protection. As additional chemicals are labeled for use on wheat seed it should be possible to reduce root disease losses by this means.

8A–2.3 Date of Seeding

Winter wheat sustains less damage from root-infecting pathogens if planting is delayed. Specific diseases that are reduced by late planting include take-all (Dolezal and Jones, 1981; Maloy and Cook, 1981), Cephalosporium stripe (Raymond and Bockus, 1984), common root and crown rot (Fenster et al., 1972), seedling blight (Slykhuis et al., 1957), Rhizoctonia root rot (Parmeter, 1970), and strawbreaker foot rot (Bruehl et al., 1974). Late planting either results in plants being exposed to weaker inoculum (take-all), plants with a reduced number of infection courts (Cephalosporium stripe), or plants exposed to pathogens which are in a state of reduced activity (take-all, seedling blight, and foot rot). Spring wheat usually is less affected by most of these diseases; however, late planting of spring wheat into warmer soils may actually increase seedling blight (Stack, 1982).

To reduce diseases significantly, winter wheat must be seeded at least several weeks after the usual seeding date; the later the better for disease control. However, in some areas such as the Great Plains, each week of delay in seeding beyond the optimum date results in about 10% reduction in yield potential in the absence of diseases (Raymond and Bockus, 1984). Thus, for these areas the benefit derived from late seeding for disease control is usually negated by the associated loss in yield potential. If more than one pathogen occurs within a field, or if there are other problems that are reduced by late seeding (wheat streak mosaic, Hessian fly), then this practice should be given greater consideration. Producers with only a small percentage of their hectarage displaying root disease problems should plant that last.

8A–2.4 Seeding Rate

Most root and crown diseases are not greatly affected by seeding rate and normal recommendations for an area should be followed. However, strawbreaker foot rot and Fusarium foot rot are reduced by lowering the seeding rate, due to reduced humidity within the canopy (strawbreaker) (Bruehl et al., 1974) and reduced competition for moisture between plants (Fusarium) (Cook, 1980). As with delayed seeding, reducing the amount

of seed planted to suppress strawbreaker foot rot may result in reduced crop yield potential (Bruehl et al., 1974), rendering this control procedure undesirable.

8A–2.5 Fertilizers

Generally speaking, a balanced fertility program for wheat production in an area should be followed. This should be aimed at promoting vigorous plant growth, especially roots, and will help reduce such diseases as Pythium root rot (Mitchell, 1946; Vanterpool, 1952), Rhizoctonia root rot (Butler, 1961), and take-all (Taylor et al., 1983). Excessive fertilizer use should not be a practice where common root and crown rot occur, as this may result in large plants which rapidly deplete the soil moisture, hence enhancing disease (Cook, 1980).

Take-all can be profoundly affected by soil fertility. Ammoniacal forms of N are preferable to nitrate forms (Huber et al., 1968) because they produce a more acidic rhizosphere pH, which inhibits the activity of the fungus (Smiley and Cook, 1973). Chloride fertilizers have also been demonstrated to reduce take-all losses by affecting plant water potential to the detriment of the pathogen (Christensen et al., 1981; Powelson and Jackson, 1978).

8A–2.6 Chemicals

In addition to seed treatments, chemicals applied during the season may reduce root, crown, and foot diseases. Strawbreaker foot rot is economically controlled with one application of a fungicide in the spring (Bruehl et al., 1974; Powelson, 1982). Controlling weeds with herbicides can conserve soil moisture, thus reducing losses from common rot and crown rot (Cook, 1980). Lime application to acid soil during the summer has been shown to greatly reduce incidence of Cephalosporium stripe in subsequent crops (Bockus and Claassen, 1985).

8A–2.7 Irrigation

Both dry and moist soil conditions can increase root and crown diseases. Take-all and Pythium root rots are favored by moist soil, and if irrigation is practiced, infrequent but deep irrigations are preferable to frequent, shallow ones. On the other hand, the mature plant phase of common root and crown rot is greatly favored by drought stress (Cook, 1980). Irrigation to reduce stress after the boot growth stage will reduce or eliminate disease loss in this case. Sharp eyespot and Rhizoctonia root rot are also favored by dry soils (Wiese, 1977). In general, irrigations should be applied to avoid drought stress, but the top few cm of soil should be allowed to dry between applications of water.

8A–2.8 Residue Disposal

Most soilborne root diseases are increased by reduced tillage practices, including Cephalosporium stripe (Bockus et al., 1983; Latin et al., 1982), take-all (Moore and Cook, 1984), Pythium root rot (Cook et al., 1980), and root-lesion nematodes. The increase in the amount of wheat residue left on or near the soil surface favors the survival and reproduction of the pathogens that cause these diseases. Moldboard plowing or disking usually results in less disease than continuous minimum-tillage or no-till wheat production; however, reduced tillage may lower strawbreaker foot rot incidence (Herrman and Wiese, 1985), although this effect may be erratic. The relatively drastic measure of burning wheat stubble greatly reduces the amount of Cephalosporium stripe by killing most of this fungus (Bockus et al., 1983). Since reduced tillage conserves fuel, soil moisture, organic matter, and soil, alternative methods of controlling these diseases should be practiced.

8A–2.9 Crop Rotation

Rotation to a crop other than small grains is an extremely effective control for many soilborne wheat diseases. Take-all, Cephalosporium stripe, and foot rot are all greatly reduced by rotation to a nonhost, since the fungi which cause these diseases die out relatively rapidly if small grains are not present. Microbial decomposition of the wheat residue harboring the pathogens during the time wheat is not grown results in markedly reduced populations because these pathogens are not soil inhabitants. Depending on the area, substantial control by this method may require a 1 to 3 yr absence of wheat (with the variation due to differences in residue decomposition rates). Pathogens that have a broad host range or survive well in soil (*Rhizoctonia* spp., *B. sorokiniana*, and *Pratylenchus* spp.) are not controlled as effectively with crop rotation. However, their populations are usually reduced by rotation (Diehl et al., 1982), and this can result in some reduction in disease. In some areas there are no suitable alternate crops, or rotation results in the loss of a cropping season; these factors will have to be weighed before a rotation schedule is implemented.

8B Bacterial and Fungal Blights of the Foliage and Heads of Wheat

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Foliar and head blight diseases cause serious losses in yield and seed quality throughout most areas of the world where wheat (*Triticum aestivum* L. em. Thell.) is grown. These diseases are usually more severe in humid areas, but some cause substantial losses in semiarid regions during wet seasons or under special production conditions such as overhead irrigation.

Changes have occurred in disease problems with changes in crop management such as the use of higher rates of N fertilization, and the use of semidwarf cultivars. Propagules of pathogens that are disseminated only short distances, usually by rain splash, have become more important on these shorter cultivars (which also have a denser leaf canopy). Furthermore, until recent years these diseases received less attention from researchers than powdery mildew, the rusts, and the smuts.

Many of the diseases discussed in this chapter are now being investigated more intensively and several have been reviewed in depth since the late 1970s. These are noted in the discussion of the individual diseases. Additionally, a number of diagnostic books with excellent color photographs have become available (CIMMYT, 1977; Wiese, 1987; Zillinsky, 1983). Some mostly older references also contain important basic information about many of the diseases (Boewe, 1960; Dickson, 1956; Jones and Clifford, 1984; Sprague, 1950). Emphasis is on important new information about these diseases since the publication of the first edition of *Wheat and Wheat Improvement* in 1967 (Quisenberry and Reitz, 1967).

The diseases caused by bacteria are discussed first. Fungal diseases are arranged primarily according to the portion of the plant which is attacked, foliage or heads. However, some pathogens attack all aerial parts, and therefore some departure from this arrangement has been necessary.

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8B–1 BACTERIAL DISEASES

Bacterial diseases cause relatively minor losses to wheat compared to diseases caused by fungi. However, these diseases have not been studied as thoroughly as those caused by fungi and losses may be greater than reported.

Recent changes in taxonomy of bacterial plant pathogens at the species level have resulted in major revisions of nomenclature. The physiology and genetics of these bacteria are active areas of study and it is likely that additional changes in nomenclature will result. Current nomenclature is according to Dye et al. (1980).

8B–1.1 Bacterial Leaf Streak or Black Chaff

Bacterial leaf streak is caused by two pathovars of *Xanthomonas campestris*. (This pathogen was formerly known as *X. translucens*.) The causal strains are classified as *X. campestris* pv. *undulosa* (J. J. & R.) Dye and *X. campestris* pv. *translucens* (J. J. & R.) Dye. Pathovar designations are based on host range. Strains pathogenic to wheat also may be pathogenic to rye (*Secale cereale* L.), triticale (X *Triticosecale* Wittmack), and in some cases barley (*Hordeum vulgare* L.) (Cunfer and Scolari, 1982). The most common name of the disease, black chaff, is somewhat misleading, because symptoms are most prominent on the leaves. The disease usually is found on the heads late in the season. When diagnosing disease on the head it is necessary to distinguish symptoms from other causes of glume discoloration such as infection by *Leptosphaeria nodorum* and UV radiation (CIMMYT, 1977).

Inoculum is seedborne and also survives in the debris of a previous susceptible crop. Bacterial cells are dispersed mainly by rain splash, but insects and wind-blown aerosols also are important. The bacterium enters the plant through natural openings and wounds. This disease is one of the easiest foliar blights to recognize on wheat. The lesions begin as very narrow (1–2 mm wide) water-soaked streaks which may elongate to the entire length of the leaf. The streaks are often oily to the touch and translucent when held to the light. Following rain or heavy dew mucoid droplets of yellow bacterial exudate cover much of the lesion. The exudate dries to form a flaky or granular coating on the leaves. Two selective media for isolation of the bacterium have been reported recently (Kim, 1983; Schaad and Forster, 1985).

Bacterial leaf streak has become more important during recent years in some areas of the western USA (Scharen et al., 1976). Organic Hg seed treatments which eliminated or greatly reduced infection by seedborne inoculum are no longer available; seed treatments now available are less effective. It is also likely that some cultivars now grown are less resistant than those grown previously.

8B–1.2 Bacterial Leaf Blight

Bacterial leaf blight, caused by *Pseudomonas syringae* pv. *syringae* Van Hall was first identified as an important wheat disease in the early 1970s (Otta, 1974, 1977). The bacterium is widely distributed in soil and lives as part of the resident bacterial population on wheat leaves. It is also seedborne. Most strains cause holcus spot on sorghum [*Sorghum bicolor* (L.) Moench] and maize (*Zea mays* L.). The population of strains is highly variable in virulence to wheat. It has been suggested that the increased prevalence of bacterial leaf blight may be due to a change in virulence of *P. syringae* or to greater susceptibility of newer cultivars (Sellam and Wilcoxson, 1976).

Leaf blight occurs in response to specific environmental conditions. These are periods of wet weather, especially driving rain (which may aid entry of the pathogen into the leaf), and temperatures between 15 and 25° C. Symptoms, which begin as minute, water-soaked spots, enlarge over several days to become irregular tan to bleached white necrotic spots and streaks. Symptoms often appear suddenly near heading stage, although none were apparent earlier. Because virulent strains reside on the leaf surface, symptoms may develop rapidly on all leaves when environmental conditions favor dissemination and growth of the bacterium (Fryda and Otta, 1978; Otta, 1974; Sellam and Wilcoxson, 1976).

The disease has been reported on both winter and spring wheat, primarily from the northern Great Plains of the USA and Canada. Cultivars vary widely in susceptibility, but resistance has been identified (Otta, 1974; Scharen et al., 1976).

8B–1.3 Basal Glume Rot

Basal glume rot is caused by *Pseudomonas syringae* pv. *atrofaciens* (McCulloch) Young, Dye & Wilkie (syn. *P. atrofaciens*) (Wilkie, 1973). It is generally a minor disease in most wheat-growing areas. However, it is considered important in the Ukraine region of the USSR. Irregular, green, water-soaked lesions develop on leaves, the peduncle, and lower portions of glumes. The lesions quickly turn brown and necrotic. Losses result from shriveled grain. Basal glume rot often caused serious losses in Canada from 1920 to 1940. Apparently, the disease has been controlled by improved cultivars. In the USSR, four serotypes are recognized (Siminovich et al., 1977). Bacteriophages also have been used to separate strains (Sutton, 1966). Symptoms on the leaves are similar to those attributed to bacterial leaf blight.

8B–1.4 Spike Blight or Tundu

Corynebacterium tritici (ex Hutchinson) Carlson & Vidaver is a serious problem only in some areas of India, although it has been reported from most wheat-growing regions. The disease it causes, variously known

as yellow slime, yellow ear rot, spike blight, or (especially in India) tundu, results when the gall nematode *Anguina tritici* transmits the bacterium. There is experimental evidence that the bacterium is unable to cause the disease without the presence of the nematode (Gupta and Swarup 1968, 1972). In some areas the bacterium may be able to invade the host alone (CIMMYT, 1977). Removal of nematode galls from seed controls the disease. A brine seed soak is recommended in India as an inexpensive method to eliminate the nematode from seed (Suryanarayana and Mukhopadhaya, 1971). Unlike similarly diseased ryegrass (*Lolium multiflorum* Lam.), infected wheat is not toxic to mammals (Bird, 1981; Vidaver, 1982). The closely related species, *C. iranicum* (ex Scharif) Carlson & Vidaver, causes similar symptoms (Carlson and Vidaver, 1982b; Vidaver, 1982).

8B–1.5 Minor Bacterial Blights

Several other bacteria cause only occasional local damage to wheat. *Corynebacterium michiganense* ssp. *tessellarius* Carlson & Vidaver was identified only recently as the cause of bacterial mosaic. Symptoms are chlorotic mosaic lesions with indefinite margins. The small individual lesions sometimes resemble those caused by *P. syringae*, but no water-soaking is observed. A unique feature of this bacterium is that wounds are not required for its entry into the host. It is also seedborne. The disease has been reported from Nebraska, Iowa, and Alaska (Carlson and Vidaver, 1982a, 1982b; McBeath and Vidaver, 1981) and from Canada (A.K. Vidaver, University of Nebraska, 1984, personal communication).

Bacillus megaterium de Bary pv. *cerealis* Hosford has been recently implicated as a possible cause of a white blotch on many of the aerial parts of wheat. Symptoms are somewhat similar to those caused by *P. syringae* pv. *syringae*. However, *B. megaterium* pv. *cerealis* causes wide spots that cover most of the leaf blade and the lesions are not watersoaked. The pathogen may be epiphytic on wheat and it is transmitted at low levels through seed. Symptoms have been extensive on many host genotypes, but economic loss has not been documented (Hosford, 1982a).

Erwinia rhapontici (Mill.) Burk. (syn. *E. carotovora* var. *rhapontici* (Mill.) Dye) causes pink seed that may be confused with scab. The bacterium invades injured seeds when grain is harvested prematurely, probably as a response to high seed moisture. The bacterium may be disseminated by a gall midge (Wiese, 1987).

8B–1.6 Discussion

Fungal and bacterial pathogens of the aerial parts of plants have one etiological characteristic in common. All require prolonged periods of free moisture for invasion of the host. Most are partly or entirely dependent upon rain for dissemination of propagules. Many of the bacterial diseases are most important in the humid wheat-growing regions. How-

ever, depending on weather conditions these diseases also may cause significant losses in semiarid regiona as well.

Bacterial pathogens have several etiological characteristics in common. They require wounds or natural openings to enter the plant, and free water is needed for growth and dissemination. Survival is often dependent on longevity of debris of the infected plants that they inhabit. Many are seedborne. Additionally, inoculum of some pathogens, such as *P. syringae*, may be present epiphytically and cause disease only under proper environmental conditions. It is becoming increasingly evident that many plant pathogenic bacteria survive and multiply on plant surfaces prior to causing disease.

Chemical control, other than seed treatment, is largely ineffective or not warranted economically. In many cases seed treatment has limited value also. Crop management and the use of resistant cultivars are the primary means of control. Resistance to bacterial diseases has probably been bred into most cultivars as part of selection against foliar diseases in general rather than as a pathogen-specific effort. Where efforts have been made to select for resistance under disease pressure it has been primarily for bacterial leaf streak.

8B–2 FUNGAL LEAF BLIGHTS

8B–2.1 *Septoria* Diseases

Several species of *Septoria* cause leaf and head blight diseases of wheat. The two most important diseases are Septoria tritici blotch and Septoria nodorum blotch (King et al., 1983; Shaner, 1981; Shipton et al., 1971). Although both pathogens are almost always encountered as the asexual (*Septoria*) stage, their taxonomic affinities are more divergent because the associated sexual stages are in different genera.

Two species of *Leptosphaeria* attack wheat. These are *L. nodorum* E. Müller [*S. nodorum* (Berk.) Berk.] and *L. avenaria* Weber f. sp. *triticea* T. Johnson (*S. avenae* Frank f. sp. *triticea* T. Johnson). Symptoms caused by both are identical and separation is made primarily by differences in the size of conidia of the *Septoria* stage. However, individual isolates overlap in this character also, and it is apparent that these species are closely related (Krüger and Hoffmann, 1978). *Leptosphaeria avenaria* f. sp. *triticea* is encountered much less frequently than *L. nodorum* and is much less important (Hosford, 1976; Hosford and Busch, 1974; Shearer & Wilcoxson, 1980).

Mycosphaerella graminicola (Fuckel) Schroeter (*S. tritici* Rob. & Desm.) causes septoria tritici blotch. The disease is confined to the leaves. The disease caused by *L. nodorum* is referred to as glume blotch because of the rapid necrosis it causes on the glumes; however, the leaves also are severely affected. During the jointing and heading stages of growth conidia of both fungi are dispersed by rain from the lower leaves through

the canopy to the upper leaves and head. Optimal temperature for disease is 20 to 25° C for both fungi; both require humid conditions for disease development (Shipton et al., 1971). Usually symptoms become progressively more severe from the lower leaves to the head as the season advances. However, at optimal temperature and when overcast weather persists for several days, a single rain can disseminate inoculum from the lower leaves to the heads of a susceptible cultivar in one step. Thus, septoria nodorum blotch may appear suddenly on the head without prior progressive symptom development on the upper leaves.

Both fungi survive as pycnidia on wheat debris; *L. nodorum* is particularly abundant on the nodes. *Leptosphaeria nodorum* is not an active saprophyte, but new pycnidia may form in colonized tissue. Survival in straw is dependent upon the deterioration rate of the straw (Scharen, 1964).

Many wild species of grasses are infected by *L. nodorum* and *M. graminicola*, but sporulation on these hosts is often limited. The role of weedy grasses as an inoculum source is not clear. Similarly, the sexual stages of both fungi are limited in occurrence and their importance in the disease cycle is uncertain (Sanderson and Hampton, 1978).

Infection of seed by *L. nodorum* may exceed 50% in humid climates and serves as a means to introduce the disease into new fields (Cunfer, 1978, 1983). Yield loss may be attributed solely to seedborne inoculum under some growing conditions (Babadoost and Hebert, 1984; Luke et al., 1985). Infection by *L. nodorum* causes the coleoptiles to be shortened, with brown streaks; often the coleoptile tissue becomes distorted into distinctive knobs (Cunfer, 1983). Infection then may proceed to the first leaf. The fungus can survive in the leaves through the winter without causing symptoms (Bannon, 1978). Seedborne inoculum is not important in drier and cooler climates when the disease does not reach the head (Shearer and Wilcoxson, 1980).

Leptosphaeria nodorum can cause severe infection of the head, but *M. graminicola*, although capable of infecting heads, rarely does so. This is due to the fact that *L. nodorum* requires only 1 to 4 h of dew period to infect, whereas *M. graminicola* requires about 20 h (Holmes and Colhoun, 1974). Because *M. graminicola* seldom invades the head, it is unlikely that the pathogen would invade the seed.

The interaction of temperature and duration of dew period influences the geographical distribution of the diseases. Septoria nodorum blotch is most severe in warm humid climates such as the southern USA. Septoria tritici blotch does not occur in much of this region but is important in the cooler midwestern and northeastern USA. *Leptosphaeria nodorum* occurs throughout the Midwest and Northeast, but causes damage only late in the season when environmental conditions are favorable. Similarly, in South America *M. graminicola* is the more important pathogen at the more southerly latitudes. *Mycosphaerella graminicola* is prevalent in the Middle East, where annual rainfall exceeds 700 mm (Saari & Wil-

coxson, 1974). *Leptosphaeria nodorum* is not a problem there because of the dry weather during the warmer portion of the season.

Resistance to *L. nodorum* appears to be quantitative. Restriction of sporulation and rate of lesion expansion are the components most highly correlated with rate-reducing or partial resistance in the field (Jeger, 1980; Jeger et al., 1983b; Rapilly, 1977).

Race specific resistance to *M. graminicola* has been reported (Eyal et al., 1973). However, quantitative resistance and tolerance are probably the most important means of resistance to Septoria tritici blotch (Eyal, 1981b; Ziv et al., 1981). Two types of resistance to Septoria tritici blotch have been recognized. One type is the resistance from 'Bulgaria 88.' It is characterized by low disease severity and extremely low numbers of pycnidia in lesions. It is controlled by one or a few genes (Shaner et al., 1975). Resistance sources controlled by 1 to 3 recessive genes (Rosielle and Brown, 1979) and in *Agropyron elongatum* have also been identified (Rillo et al., 1970). The second type is expressed as having little necrosis on the upper two leaves although the lower leaves may be severely diseased and have an intermediate number of pycnidia in lesions (Shaner et al., 1975). This resistance apparently is expressed as a combination of reduced inoculum potential and reduced rate of development of necrosis. It is also usually associated with delayed maturity (Rosielle, 1972). Late maturity, often interacting with tall plant stature, has also been associated with resistance to both *L. nodorum* and *M. graminicola* (Eyal, 1981a; Nelson et al., 1974; Scott et al., 1982). Warmer temperatures occurring later in the season are unfavorable for both diseases. In the southeastern USA at least, the latter 4 to 6 weeks of the growing season are often dry as well as warm. Therefore, late-maturing cultivars often escape the wet conditions necessary for development of septoria nodorum blotch.

8B–2.2 Tan Spot or Yellow Leaf Spot

Pyrenophora trichostoma (Fr.) Fckl. [syn. *P. tritici-repentis* (Died. Drechs)] has been recognized increasingly as an important leaf spot pathogen in the Great Plains region of North America and in eastern Australia (Hosford, 1971, 1972, 1982b; Khan et al., 1971; Rees and Platz, 1979). The disease it causes is known variously as yellow leaf spot or tan spot. Shaner (1981) presents a concise summary of the epidemiology of the disease. The symptoms, irregular, coalescing light tan spots surrounded by chlorosis, are similar to those caused by *Septoria* fungi. Tan spot often occurs as a complex with *L. nodorum* or *L. avenaria* f. sp. *triticea* (Hosford & Busch, 1974; Khan et al., 1971). Tan spot has become an increasing problem where continuous cropping of wheat in combination with reduced tillage is practiced. Crop debris remaining on the soil surface has consistently been associated with significant yield losses (Rees and Platz, 1979; Watkins et al., 1978).

Ascospores from pseudothecia which overwinter on wheat stubble initiate epidemics. Cool, wet weather favors spore release and infection.

The asexual stage is *Drechslera tritici-repentis* (Died.) Shoem. (syn. *Helminthosporium tritici-repentis* Died.). Its role as inoculum varies with environmental conditions. If wet weather persists through the heading stage abundant conidia are produced on leaf lesions and remaining crop residue. These conidia initiate secondary disease cycles which then contribute significantly to yield loss (Rees and Platz, 1980). The disease is most severe from the boot to the dough stage, with damage being greatest on late tillers. Thousand-kernel weight is reduced and as much as 48% reduction in yield has been reported in Australia (Rees and Platz, 1983). Dry weather delays and reduces sporulation so that secondary cycles contribute little to the epidemic (Hosford, 1972). Sporulation is dense only on senescent mature tissue. The asexual spores are wind-blown for long distances. Hosford and Busch (1974) have suggested that conidia on maturing crops to the south produce inoculum for later maturing crops farther north.

The fungus is highly variable. Wheat cultivars differ in susceptibility, which is partly related to duration of the dew period. Resistance of some cultivars may be overcome by prolonged periods of moisture (Hosford and Busch, 1974).

8B–2.3 Helminthosporium Leaf Blight

Cochliobolus sativus (Ito & Kurib.) Drechsl. ex Dastur, asexual stage, *Bipolaris sorokiniana* (Sacc. in Sorok.) Shoem. (syn. *Helminthosporium sativum*, *Drechslera sativa*), causes a leaf blight of wheat which is usually less severe than spot blotch caused by this fungus on barley. *Cochliobolus sativus* has a wide host range which also includes many grasses. Conidia from the leaf blight phase serve as inoculum for head and seed blight later in the season (Shaner, 1981).

The fungus consists of two mating types. The sexual stage forms readily in vitro, enabling study of the inheritance of pathogenicity and formation of the sexual stage. Pathogenicity to wheat is governed by two to four genes and virulence is epistatic to avirulence. The genes are widely distributed among isolates from a broad geographic range (Hosford et al., 1975). A similar pattern was observed for genes governing formation of the perithecium and ascospores (Harding and Tinline, 1983). Kline and Nelson (1971) also determined that pathogenicity of *C. sativus* from barley was simply inherited and governed by one or two genes.

8B–2.4 Alternaria Leaf Blight

Alternaria triticina Prasada & Prabhu causes a serious leafspot of wheat in India (Prabhu & Prasada, 1966). It has not been reported from other areas of the world. Lesions are irregular in size, with chlorotic margins. The center of the lesions becomes brown and necrotic, and dark conidia develop profusely on them during periods of moisture. The symptoms may be confused with those caused by *C. sativus*. The heads and

kernel may also be invaded. Unlike *A. tenuis*, *A. triticina* colonizes the entire seed and therefore infected seed is an important source of inoculum. The disease became important following the release of susceptible cultivars. The disease has been controlled by resistance.

8B–2.5 Minor Fungal Leaf Blights

Downy mildew caused by *Sclerophthora macrospora* (Sacc.) T. S. & N. (syn. *Sclerospora graminicola* (Sacc.) Schroet., *S. macrospora* Sacc.), occurs rarely, although it has been reported from most wheat-growing areas. Very wet conditions are most conducive for infection. Standing water in low areas from rain or irrigation permits release and dissemination of infective motile zoospores. Diseased plants are stunted and have greatly distorted leaves and heads which usually produce no grain (Saari & Wilcoxson, 1974; Troutman & Matejka, 1972).

Fusarium nivale (Fr.) Ces. (sexual stage *Calonectria nivalis* Schaf.) is usually encountered as a snow mold pathogen, although it infrequently causes blighting of the leaves and head. Leaf infections may be associated with prior infection by other pathogens or with wounds (Forrer et al., 1982). It has been recorded once as the cause of an extensive leaf blight on wheat in Scotland and on triticale in Mexico at sites where cool weather occurs throughout the growing season (Richardson and Zillinsky, 1972). *Fusarium nivale* causes a leaf and head blight in the Yangtze River region of China. Infection is initiated by ascospores on the lower leaf sheaths (Nelson et al., 1981).

Ascochyta tritici has been reported infrequently as a pathogen of wheat. The fungus was associated with irregular to spindle-shaped chlorotic spots somewhat similar to those caused by wheat spindle streak mosaic virus. Older lesions resemble those caused by *Leptosphaeria nodorum*. Although *A. tritici* apparently is widely distributed, it is of little economic importance (Scharen and Krupinsky, 1971).

Platyspora pentamera is a very weak pathogen of wheat. It is found only infrequently in the northern Great Plains of the USA. The fungus causes irregular yellow to light brown spots on leaves. The fungus survives on plant debris and other grasses and cereals (Hosford, 1976).

Other fungi which have been noted rarely as leaf blight pathogens are *Phoma glomerata* (Hosford, 1975), *P. insidiosa* (Nema et al., 1971), *Phyllachora graminis* causing tar spot (Wiese, 1977), and *Selenophoma donacis* (Sprague, 1950). Saari and Wilcoxson (1974) have briefly summarized their observations of various leaf spot diseases in Asia and Africa.

8B–3 FUNGAL HEAD BLIGHTS

8B–3.1 Scab or Head Blight

Scab or head blight is caused by the ascomycete *Gibberella zeae* (Schw.) Petch. Several systems of nomenclature have been used for the asexual

(conidial) stage of the scab fungus. The two designations in current use are *Fusarium graminearum* Schwabe and *F. roseum* Link emend. Snyd. & Hans. 'Graminearum' (Nelson et al., 1981, 1983). Other closely related Fusaria, *F. culmorum*, *F. avenaceum*, and *F. nivale* also contribute to the head blight complex, but are generally less important than *F. graminearum*.

Gibberella zeae manifests its pathogenic potential in several ways. It has been subdivided into two populations based on characteristics of the *F. graminearum* stage. *Group I* isolates are associated primarily with crown rot of wheat and rarely produce the *Gibberella* stage. They can cause scab during abnormally wet weather in the semiarid regions where this pathogen is most commonly found (Nelson et al., 1981). *Group II* isolates are associated with head blight of wheat and stalk rot of maize in humid climates. These isolates produce the *Gibberella* stage (Francis and Burgess, 1977; Purss, 1971). Comprehensive reviews of the diseases on both crops have been presented by Sutton (1982) and Martin and Johnston (1982).

Prolonged wet periods during the flowering period are critical to infection. Infection begins almost exclusively on the extruded anthers. Wheat is less susceptible prior to anthesis and after flowering. Anther tissue is high in choline and glycinebetaine, which greatly stimulate the growth of *G. zeae* (Pearce et al., 1976; Strange and Smith, 1971, 1978; Strange et al., 1974). These compounds occur at much lower concentrations in other wheat tissues and also stimulate *F. avenaceum* and *F. culmorum* (Strange and Smith, 1978). Losses are enhanced if rain is abundant at the late stages of ripening and if harvest is delayed because of rain.

Because of the short period of high susceptibility there is usually only one infection cycle, with inoculum arising from crop debris of the previous season. Both the *Gibberella* and *Fusarium* stages serve as inoculum. *Fusarium* macroconidia form during free moisture conditions, whereas perithecia form during periods of water stress (-1.5 MPa water potential) in vitro (Sung and Cook, 1981).

The fungus therefore can produce inoculum under diverse moisture conditions. Survival of the pathogen is associated almost entirely with crop residue and infected seed. Reduced tillage may lead to increased incidence of scab because of the greater quantity of residue on which inoculum can be produced.

Yield reduction comes from reduced test weight and number of kernels. Even when yield reduction is low, great losses can occur because the fungus produces potent animal toxins during colonization of the seed. The most important of these are the estrogenic toxin zearelenone (F-2) and the trichothecene deoxynivalenol (vomitoxin). If one or both of these toxins are present, a grain lot may be graded down or rejected entirely in commerce. The other *Fusarium* spp. which may contribute to head blight produce much less or no toxin. Zearalenone also acts as a fungal hormone that stimulates development of the *Gibberella* stage. Perithe-

cium formation is inhibited by the insecticide dichlorvos (Vapona, 2,2-dichlorovinyl dimethyl phosphate) (Wolf et al., 1972; Wolf and Mirocha, 1973).

Selection of lines with resistance has been reported, but because resistance levels are low this method of control has had limited success (Martin and Johnston, 1982). Strange et al. (1978) have recommended that selection of lines with short flowering periods may be an easily used method to improve resistance. Additionally, lines with low choline and betaine in the germ may be correlated with resistance.

Management practices which reduce crop debris are probably most effective in reducing disease. These include deep plowing and rotation with noncereal crops. Because maize is also susceptible to *G. zeae*, the disease may be controlled by avoiding consecutive planting of maize and wheat (Martin and Johnston, 1982; Dickson, 1956). In humid areas of the People's Republic of China the *Gibberella* stage is produced on rice (*Oryza sativa* L.) stems, although the fungus does not cause disease on rice. Rice therefore plays the same role in providing inoculum as maize in the US Corn Belt (Nelson et al., 1981; Zhu and Guso, 1981).

8B–3.2 Black Point

Many fungi invade wheat caryopses at various stages of development. Several may cause a darkening of the pericarp, usually at the lower or germ end of the kernel. In the North Central region of North America the most important cause of black point is *Cochliobolus sativus*. This is the head blight phase of the root rot and leaf blight complex caused by this fungus. In this region *Alternaria alternata* also causes black point. However, *C. sativus* is the more aggressive pathogen. When it invades the kernel first it largely excludes other fungi (Huguelet and Kiesling, 1973). Seed infected by *C. sativus* is a major inoculum source for the seedling and root rot phase of the disease. Durum wheat is generally more susceptible than hard red spring wheat. Progress toward selection for resistance was improved by inoculating excised green kernels under controlled laboratory conditions (Statler et al., 1975).

Alternaria tenuis is primarily associated with black point in India (Bhowmik, 1969) and Australia (Shipton and Chambers, 1966), where *C. sativus* is much less important. *Alternaria tenuis* is only weakly parasitic and invades only the pericarp near grain maturity; it has little effect on seed germination (Prabhu and Prasada, 1966; Adlakha and Joshi, 1974).

Yield loss occurs from reduction in grain quality and weight. *Cochliobolus sativus* causes the greatest reduction in seed weight among the fungi causing black point. This is partly due to the infection of the glumes and the leaf blight that it causes. Fortunately, these fungi produce no mammalian toxins; contaminated grain can be fed to animals without danger.

Ultraviolet radiation causes a striping and darkening of the glumes on certain lines, particularly those with 'Hope' or 'H-44' in the pedigree.

The symptoms may be confused with those of several head pathogens. It occurs mostly at higher elevations where UV radiation is more intense (CIMMYT, 1977).

8B–3.3 Ergot

Ergot, caused by *Claviceps purpurea* (Fr.) Tul., is most serious on rye, but is occasionally important on wheat. Ergot seldom causes significant yield losses. Its seriousness lies in the potent toxins present in its resting structure, the sclerotium. Ergot toxicology has been investigated intensively and numerous reviews are available (Van Rensburg and Altenkirk, 1974).

Ergot has become more important on male sterile lines used for the production of hybrid wheat seed because *C. purpurea* infects only the unfertilized ovary. Because self-pollination of wheat occurs within the closed florets, inoculum is physically excluded from the infection court. Male sterility favors infection because the ovaries swell and the florets open, providing ready entry for spores. Prolonged periods of cool and particularly wet weather extend the period of anthesis, thus delaying fertilization and extending the infection period. The fungus completely replaces the ovarian tissue, but maintains a distinct interface with the host vascular tissue of the rachilla (Luttrell, 1980; Shaw and Mantle, 1980).

Shortly following fertilization the plant is immune to ergot (Cunfer et al., 1975; Darlington and Mathre, 1976). Few host–pathogen interactions exhibit such dramatic and rapid shifts from susceptibility to resistance.

The host range of *C. purpurea* is wide, encompassing many of the wild grasses associated with wheat production. Sclerotia overwinter in the soil and produce fertile ascostromata throughout the flowering period of grasses and small grains. The peak of ascospore release occurs before anthesis in wheat, but coincides with that of various suceptible wild grasses (Mantle, 1981; Mantle and Shaw, 1976; Wood and Coley-Smith, 1982). Infection of grassy weeds by ascospores is followed 1 to 2 weeks later by the copious production of the conidia in the honeydew stage. Conidia are disseminated readily by rain and insects to florets of susceptible hosts, including wheat, just reaching anthesis. Secondary cycles of infection continue from honeydew as long as susceptible florets are available. Mantle et al. (1977) determined that in Britain *Alopecurus myosuroides* (blackgrass) is the most important grass providing both ascospore and conidial inoculum for the infection of wheat. Ryegrass is not an important intermediate host. Conversely, in Australia, ryegrass is an important inoculum source for wheat (Bretag and Merriman, 1981). These examples illustrate the diversity of the fungus for host adaptation.

Resistance to ergot has been difficult to identify, but progress has been made in recent years. Durum wheat is more susceptible than common spring wheat but some lines of both kinds of wheat are resistant (Darlington and Mathre, 1976; Platford and Bernier, 1970, 1976; Platford

et al., 1977). Resistance in the female parent confers resistance to the progeny, probably because only the ovarian tissue is parasitized (Darlington and Mathre, 1976).

Although ergot is often thought to be found wherever small grains are produced, it may be absent in regions with mild, humid winters when small grains are planted in the fall. Ungerminated sclerotia do not survive more than 3 to 4 months in areas with mild winters where soil microbes and insects are active during the winter. For example, although rye is extremely susceptible and is grown extensively throughout Georgia, ergot is never encountered, even when sclerotia are occasionally introduced with seed. Similarly, the disease is not found on wheat in the southeastern USA (Cunfer and Seckinger, 1977).

Some natural biological control of the disease occurs. Several fungi, most notably *Fusarium heterosporum*, inhibit formation of sclerotia or decay sclerotia during overwintering (Cunfer, 1975; Mower et al., 1975).

8B–3.4 Discussion

Changes in the prevalence and importance of diseases are often related to changes in cultural practices. Host debris is a major vehicle for survival for many of the pathogens discussed in this chapter. Moldboard plowing or other means of returning wheat stubble to the soil significantly reduces inoculum by promoting deterioration of the organic matter on which many pathogens survive or grow. Additionally, some fungi require light for sporulation. Therefore, even if a fungus is able to grow on buried debris its inoculum potential is decreased greatly, because sporulation is not possible. Examples are *G. zeae* and *L. nodorum*. Widespread adoption of reduced tillage agriculture for savings in energy use and soil and water conservation also can result in significant shifts in disease problems. It is even more important when rotation with other crops is decreased and control of volunteer wheat is incomplete. The tan spot disease is a good example. It has become increasingly important where reduced tillage combined with continuous wheat production is practiced. Crop rotation remains a major means of cultural control. This is due to the association of many pathogens with crop debris and short distances of dissemination of propagules. For many of the diseases, inoculum originates at the site where the crop is grown. Changes in the importance of certain diseases will also necessitate changes in selection for resistance in wheat breeding programs.

Overhead irrigation of wheat in semiarid areas has caused an increase in foliar and spike diseases. Increases in bacterial leaf streak and Alternaria leaf blight are examples.

There has been a change in recent years in the approach to breeding techniques for selection of genotypes with disease resistance. The emphasis has been away from major gene or vertical resistance, which is often short-lived or in many cases not available. Increasing effort has been directed toward resistance mechanisms that are variously called

minor gene, *rate-reducing*, *partial*, *quantitative*, or *horizontal resistance*. The definitions of these concepts may differ somewhat, but all involve identification of resistance components which are relatively small in effect. Partial resistance reduces the rate of the epidemic, especially during the critical heading to dough stage of plant growth. These components are often difficult to quantify. Most are postulated to be controlled by a number of genes. However, advances have been made in the means of quantifying the effects. Recent work by Jeger et al. (1981, 1983a, 1983b) on *L. nodorum* is noteworthy. This approach emphasizes the important need to integrate epidemiological data into selection criteria for disease resistance.

The planting of cultivar mixtures of similar maturity but differing disease resistances also has the objective of reducing the rate of disease build-up until the critical stages of growth have been completed. This approach has been successful for control of powdery mildew of barley in Britain and may have applicability for other foliar diseases in the future.

The period of host susceptibility influences epidemiology of a disease and thus pinpoints control strategies, particularly by cultural and chemical means. These means of control become even more important when resistance is not highly effective. Scab and ergot are two diseases which illustrate this.

A recent development is the prospect for control of foliar diseases by systemic fungicides applied as seed treatments. Most of the compounds are effective for about 1 to 2 months. This may reduce early season infection of spring wheats and the autumn infection phase in winter wheats. Disease control is effected by reducing inoculum and delaying development of the epidemic until later in the season. Many of these compounds are also effective against pathogens which have a seedborne phase such as *C. sativus* and *G. zeae*.

There are a myriad of potential disease problems in wheat under varying environmental and cropping systems. It will be increasingly necessary to diagnose diseases accurately and determine precisely whether economic losses are incurred. In this way the number of diseases for which controls are needed can be identified and appropriate measures developed.

8C Rusts, Smuts, and Powdery Mildew

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The rust, smut, and powdery mildew diseases of wheat are frequently grouped together because of the highly specialized nature of pathogenicity of the causal fungi. The rusts and powdery mildew are caused by fungi that are *biotrophs*, obligately parasitic on their living host plants (although some rust fungi have been artificially cultured to a limited degree in recent years) (Maclean, 1982; Williams, 1984). The smut fungi, although found to be culturable on artificial media a century ago, possess similar highly specific relationships to host cultivars. These groups of parasites epitomize the gene-for-gene concept of host–parasite specificity that was first delineated by Flor (1971) for flax rust.

8C–1 WHEAT RUSTS

The rusts are still the most important diseases of wheat worldwide, in spite of the great progress made in their control in many countries (Saari and Prescott, 1985). Their wide distribution, their capacity to vary so as to attack previously resistant cultivars, their effective long-distance dissemination, their potential to cause a very rapid rate of disease increase, and the losses that they cause provide for this prime importance.

8C–1.1 Diseases

There are three rust diseases of wheat: stem (or black) rust, leaf (or brown) rust, and stripe (or yellow) rust (Loegering, 1967; Johnston, 1967; Hendrix, 1967; Wiese, 1987). These are conspicuous, striking-appearing, epidemic diseases affecting the foliage of the plants and causing severe losses under epidemic conditions. As a result, they were among the earliest recognized of the diseases of wheat (Arthur, 1929; Chester, 1946; Schafer et al., 1984).

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8C-1.1.1 Descriptions

8C-1.1.1.1 Stem Rust. Elongate, reddish brown pustules are evident on the stems, sheaths, and peduncles of the plants (Fig. 8C–1). They are less frequently found on the leaf blades, thus the name *stem rust*. The epidermis is raggedly ruptured by the pustules, giving the stems and sheaths a rough-textured surface. These characteristics, along with the large size of the pustules, distinguish stem rust from the other two wheat rusts. Large pustules on leaf blades may have a diamond shape. As the pustules age, they turn blackish, leading to the more commonly used European name *black rust*. See Roelfs (1985a) for an expanded presentation.

8C-1.1.1.2 Leaf Rust. Pustules of this disease are nearly the same color as those of stem rust but lighter and more orange or brown, leading to the synonyms *brown rust* or *orange rust*. They are smaller and commonly oval-shaped, being most evident on the leaf blades, hence the name *leaf rust* (Fig. 8C–2). The epidermis is not so raggedly ruptured, and the pustules usually erupt only on one leaf surface, usually the upper, in contrast to stem rust, which ruptures both surfaces when occurring on blades. See Samborski (1985) for an expanded presentation.

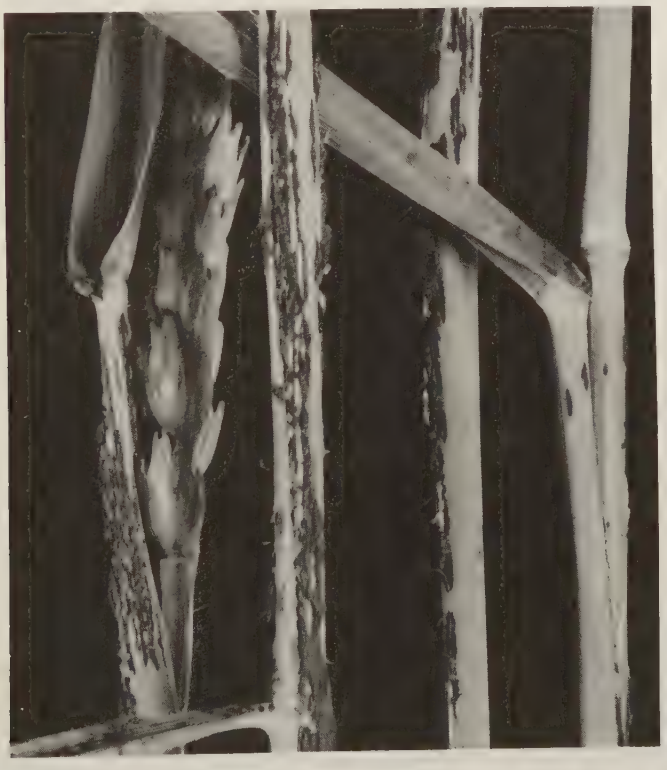

Fig. 8C–1. Wheat stem rust.

Fig. 8C–2. Wheat leaf rust.

8C–1.1.1.3 Stripe Rust. Pustules occur in a linear arrangement and are light yellow, providing the basis for the American name *stripe rust* and the common European name *yellow rust* (Fig. 8C–3). The linear arrangement is the result of a localized semisystemic infection, limited in lateral spread by the vascular bundles, but reaching several centimeters in length in early infections on susceptible cultivars. Blades, sheaths, glumes, lemmas, awns, and even immature kernels may be infected, as well as culm tissue to a lesser extent. See Stubbs (1985) for an expanded presentation.

Detailed descriptions of the signs and symptoms of these diseases are provided by Loegering (1967), Johnston (1967), and Hendrix (1967) in the first edition of the present work and by Wiese (1987) in a compendium of all wheat diseases. Technical descriptions of the fungi are given by Cummins (1971) and Savile (1984) in their taxonomic treatments.

8C–1.1.2 Early History

Kislev (1982) reported archaeological evidence of wheat lemma fragments with stem rust pustules which were dated between 1400 and 1200 B.C. There are ancient written observations of wheat diseases in biblical sources and Greek and Roman writings. These have been related to various modern diseases, including the rusts (Arthur, 1929; Chester, 1946).

Fig. 8C–3. Wheat stripe rust.

Savile and Urban (1982) recounted the evolution of stem rust with respect to the human-guided evolution of its hosts. Wheat rusts have undoubtedly been present throughout the development of wheat and related grasses over the time span of their evolution.

The first scientific presentations on wheat rusts are those of Targioni Tozzetti (1767) and Fontana (1767), both in Florence, Italy, following a severe epidemic on the crop in 1766. Targioni Tozzetti stated that "the rust was universal over the whole of Italy" and that it "is a very ancient scourge of the greater part of the country cultivated by mankind in the old world." Fontana, in turn, reported "that the rust . . . had devastated the lands of Tuscany." Such severely epidemic years have occurred irregularly throughout history in the wheat-growing regions of the world in years when environmental conditions were particularly favorable. In the USA the most notorious early years for stem rust, the most damaging of the wheat rusts, were 1878 (Hamilton, 1939), 1904, and 1916 (Loe-

gering, 1967). The 1904 epidemic stimulated the initiation of breeding for rust resistance in U.S. wheat programs, and the 1916 epidemic was the motivation for eradication of the alternate host, barberry (*Berberis* spp.), in the USA (Roelfs, 1982).

8C-1.1.3 Crop Production Limitation

The ancient Greek literature gives clear indications that rusts of cereals were destructively epidemic (Stakman and Harrar, 1957). Rust diseases were also considered damaging in the early years of American agriculture. The U.S. epidemic of 1916 was estimated to have prevented production of 182 million bu (38%) of the potential total wheat crop of the country (Loegering, 1967). Because of the devastating effects of the rusts on the wheat crop, estimates of yield limitation (losses) have been systematically made in many states in the USA since 1918. These were summarized for the period from 1918 to 1976 by Roelfs (1978). He noted that stem rust historically produced the most serious rust epidemics in the USA. However, leaf rust causes losses more regularly.

8C-1.1.3.1 Stem Rust. Stem rust has been of greatest importance, and in earlier years, caused the greatest losses in the spring wheat region of the north central states and adjacent Canada. Roelfs' data (1978) show routine moderate epidemics in this region from 1919 through 1927 (e.g., losses in North Dakota, South Dakota, and Minnesota of 10–30% in 5 or 6 yr of the 9-yr period). By the end of this time, significant numbers of barberry were eradicated (Roelfs, 1982), effectively removing this common alternate host as a source of inoculum. Subsequently, years of major loss have been much more sporadic and rare. For comparison, from 1918 through 1929 a 10% loss to stem rust occurred in some state of the USA in 8 of these 12 yr, whereas from 1930 through 1982 a 10% loss to stem rust occurred in some state in only 8 of these 53 yr. This change in frequency of epidemic years, occurring about 1930, appears largely attributable to the effectiveness of barberry eradication in the removal of early season inoculum.

Nevertheless, stem rust continued to be very severe in some years of this more recent period, with the greatest single statewide loss estimated at 57% in North Dakota, a major wheat-growing state, in 1935. These later severe but infrequent losses were more regional or national in scope and appear due to regional or continental epidemics, initiated by airborne inoculum in favorable years. However, since 1965 stem rust losses in the USA have been insignificant, and in the spring wheat region, the historic stem rust epidemic area, almost lacking since 1954. This second-step, near elimination of losses now for two to three decades, appears in turn due to the use of effective host resistance, superimposed on the prior alternate-host eradication.

8C-1.1.3.2 Leaf Rust. Reitz and Salmon (1959) calculated that significant losses from leaf rust occurred in 7 yr out of 10 in the Hard

Red Winter wheat region of the central and southern Great Plains, with heavy losses 1 yr out of 10. Inhibition of the yield potential up to 70% has been demonstrated experimentally (Johnston, 1967). Important losses from leaf rust have continued to the mid-1980s in the USA, with the most severe in the South and the Pacific Northwest (D.L. Long, unpublished data). The most severe single statewide report was a 50% loss in Georgia in 1972 (Nelson et al., 1972; Roelfs, 1978). Samborski (1985) stated that although leaf rust usually does not cause spectacular damage, it probably results in greater total loss than the other wheat rusts because of its broad climatic adaptation and widespread occurrence. Because of its more intermediate temperature requirements (lower than stem rust, higher than stripe rust), its epidemic losses have been more frequent on winter wheats than on the later maturing spring wheats, which are more subject to stem rust.

Joshi (1980) reported the occurrence of major leaf rust epidemics in 1972 and 1973 in India. Losses in three Indian states in the epidemic region ranged from 6 to 12%. Dubin and Torres (1981), in describing significant fungicidal control of leaf rust in northwestern Mexico in a major incipient epidemic in 1977, reported areawide losses of 40% in the Carrizo Valley on irrigated susceptible wheat where fungicides were not used.

8C-1.1.3.3 Stripe Rust. Whereas stem rust earlier caused the greatest losses in the north central spring wheat region and leaf rust on the more southerly winter wheats, losses in the USA from stripe rust have been largely in the West, where it is favored by lower temperatures. Following its recognition in 1915 and subsequent occurrence through the mid-1930s (Bever, 1937), stripe rust was of only minor importance until 1960. At that time 2 successive epidemic yr were estimated by Hendrix (1967) to have caused major losses of 12 million and 25 million bu, respectively, in the Pacific Northwest. Experimental yield limitations ranging up to 65% of potential have been reported (Bever, 1937; McNeal and Sharp, 1963; Stewart and Hehn, 1967; Doling and Doodson, 1968). Losses have continued to occur since the 1960s in that region (D.L. Long, unpublished data).

LeClerg et al. (1965) in a broadly based agricultural loss study for the period of 1951 to 1960 in the USA described the rusts as the most destructive diseases of wheat and tabulated total losses for the U.S. wheat crop for stem rust at 4%, leaf rust at 2.5%, and stripe rust at 0.1%. This period included some of the last major U.S. stem rust epidemics before the current era of effective control and was largely prior to the more recent stripe rust occurrences.

8C-1.2 Pathogens

8C-1.2.1 Taxonomy

The pathogens causing the rust diseases of wheat are members of the fungus order Uredinales, which is synonomous with the term *rust fungi*.

These are all obligate parasites on plants. Cummins and Hiratsuka (1983) divided this order into 14 families and 105 genera, the largest of which is *Puccinia* with some 3000 to 4000 species (Littlefield, 1981).

8C–1.2.1.1 Stem Rust. Wheat stem rust is caused by a sub-group of one of these species, *Puccinia graminis* Pers. ssp. *graminis* var. *graminis*, that typically attacks the grass genera *Triticum, Aegilops,* and *Elymus* (Cummins, 1971) but may also attack *Agropyron, Secale,* and *Hordeum* (Savile, 1984). Urediniospores, found in the pustules on wheat, are oblong, golden brown, with an echinulate surface and equatorial germ pores. The species is quite distinct from other rust fungi. Two subspecies are separated primarily on the length of urediniospores, as are the two varieties of subspecies *graminis* (Cummins, 1971). The specialized form attacking wheat is described pathogenically as *P. graminis* f. sp. *tritici* Eriks. and E. Henn. (Loegering, 1967). As defined pathogenically, this forma specialis appears to be generally equivalent to the taxonomically defined variety *graminis.*

8C–1.2.1.2 Leaf Rust. Wheat leaf rust is caused by *Puccinia recondita* Rob. ex Desm. This is considered by Cummins (1971) as a species complex with considerable but continuous variation. It has a very wide host range. Urediniospores are rounded (broadly ellipsoid), cinnamon brown, echinulate, and with scattered germ pores. The specialized form attacking wheat is *P. recondita* f. sp. *tritici* as described by Mains (Samborski, 1985). Savile (1984), in contrast, considered the wheat form to be a distinct species rather than a forma specialis of *P. recondita.* This is designated *P. triticina* Eriks.

8C–1.2.1.3 Stripe Rust. Wheat stripe rust is caused by *Puccinia striiformis* West. var. *striiformis* (Cummins, 1971; Savile, 1984). This variety includes the pathogenically specialized form on wheat, *P. striiformis* f. sp. *tritici,* as well as the form attacking barley and some other hosts (Stubbs, 1985). Urediniospores are broadly ellipsoid, pale yellowish to nearly colorless (because of the absence of wall pigmentation), echinulate, and with scattered germ pores.

8C–1.2.2 Life Cycles

The rust fungi are obligate parasites of their living host plants although a few species have now been artificially cultured on laboratory media (Maclean, 1982; Williams, 1984). They possess up to five different spore stages in their life cycles (Littlefield, 1981). The spore-bearing infection structures and spores they produce are designated by Cummins and Hiratsuka (1983) as: (O) Spermogonia/Spermatia: haploid male gametes, also known as pycnia and pycniospores; (I) Aecia/Aeciospores: nonrepeating spores produced by dikaryotization of spermogonia, associated with spermogonia, and giving rise to dikaryotic mycelia; (II) Uredinia/Urediniospores: repeating asexual, dikaryotic spores produced on

dikaryotic mycelia; (III) Telia/Teliospores: those spores producing basidia rather than infection hyphae; and (IV) Basidia/Basidiospores: monokaryotic spores produced, through meiosis, on basidia. See Fig. 8C–4.

There are three basic types of life cycles of rust fungi, depending on the number of spore stages occurring: macrocyclic, demicyclic, and microcyclic (Cummins and Hiratsuka, 1983). The macrocyclic form possesses all spore stages delineated above. Such rusts may be host alternating (heteroecious) or nonalternating (autoecious). *Puccinia graminis* and *P. recondita* are host alternating as well as long cycled, so may be designated as heteromacrocyclic (Fig. 8C–5). In all three wheat rust species the uredinial and telial stages occur on wheat. The other spore stages and possible alternate host have never been found for *P. striiformis*. This occurrence is sometimes referred to as a hemi-form (Stubbs, 1985). The relationship between uredinia and telia was first established for *P. graminis* by Tulasne in France in 1854 (Schafer et al., 1984). The alternation of hosts in the life cycles of the cereal rust fungi was established by de Bary in Germany, from a series of cultural experiments during the 1860s (Arthur, 1929).

The alternate hosts for *P. graminis* (stem rust) include certain species of *Berberis* (barberry) and *Mahonia* (Oregon grape) (Loegering, 1967). Prior to the extensive barberry eradication program in the USA, the more common hosts for the spermogonial and aecial states were *B. vulgaris* L., a common yard ornamental introduced from Europe, and *B. canadensis* Mill. and *B. fendleri* Gray, both native species (Loegering, 1967).

Hosts for the spermogonial and aecial stages for *P. recondita* f. sp. *tritici* (leaf rust) may include species of *Thalictrum* (meadow rue) and *Isopyrum* in the Ranunculaceae and of *Anchusa, Lycopsis*, and *Echinospermum* in the Boraginaceae (Johnston, 1967; Zadoks and Bouwman, 1985). Susceptible species of these genera having significance in the life cycle of the leaf rust form occurring on wheat are not known to occur in the Western Hemisphere, although there are limited reports of natural or experimental infection. Thus, this phase of the life cycle does not occur in the epidemiology of wheat leaf rust in North America.

Puccinia striiformis has no known alternate host. Because only uredinia and telia occur on wheat, with no spermogonia or aecia, this rust is not autoecious. This implies a heteromacrocycle for which the other phase of the macrocycle either does not now occur or merely has not been found.

The urediniospores of all three species, which occur on wheat and are infective to wheat, are thus the repeating spore stage, and provide for successive infections as long as the host is present and environmental conditions are adequate. In the virtual absence of alternate hosts in most North American wheat areas, now for all three species, the basidiospores which are produced on the basidia growing from the overwintered teliospores on wheat straw have no susceptible host to infect and are a dead end. There are in turn no aeciospores from an alternate host to infect wheat. Limited exception to this for stem rust occurs only in the

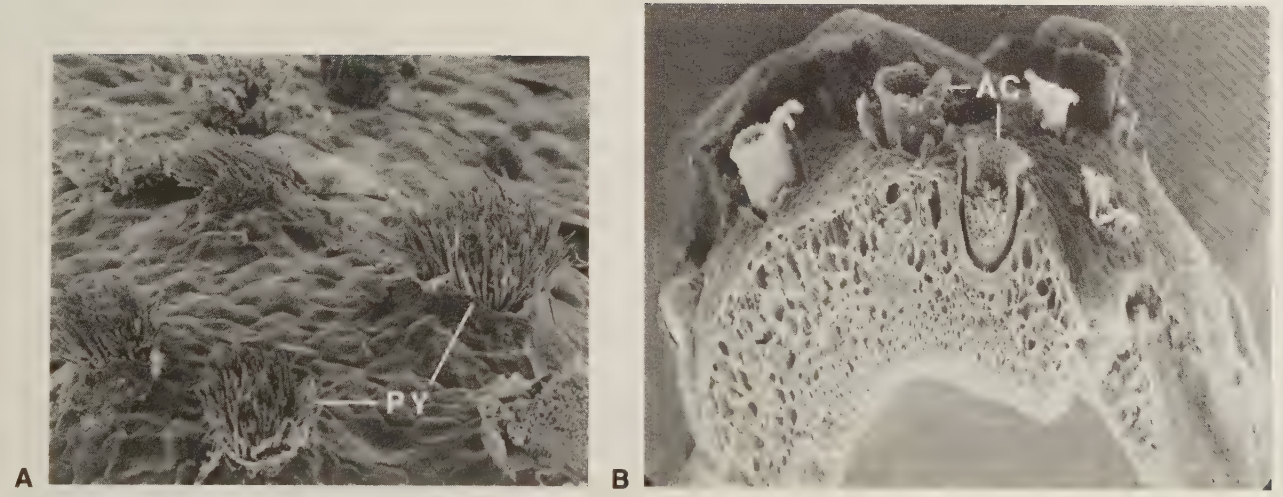

Fig. 8C–4A. Spermogonia (PY) of *Puccinia recondita*. (Photo by R. E. Gold, reprinted by permission from *Biology of Plant Rusts* by L. J. Littlefield (c) 1981, by the Iowa State University Press, Ames, IA. *Fig. 8C–4B.* Aecia (AC) of *Puccinia graminis*. (Reprinted by permission from *Biology of Plant Rusts* by L.J. Littlefield (c) 1981, by the Iowa State University Press.) *Fig. 8C–4C.* Uredinia of *Puccinia recondita*. (Photo by M.F. Brown and H.G. Brotzman, from M.V. Wiese 1977, *Compendium of Wheat Diseases*. Reprinted by permission of the American Phytopathological Society, St. Paul.)

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Fig. 8C–4. Continued.

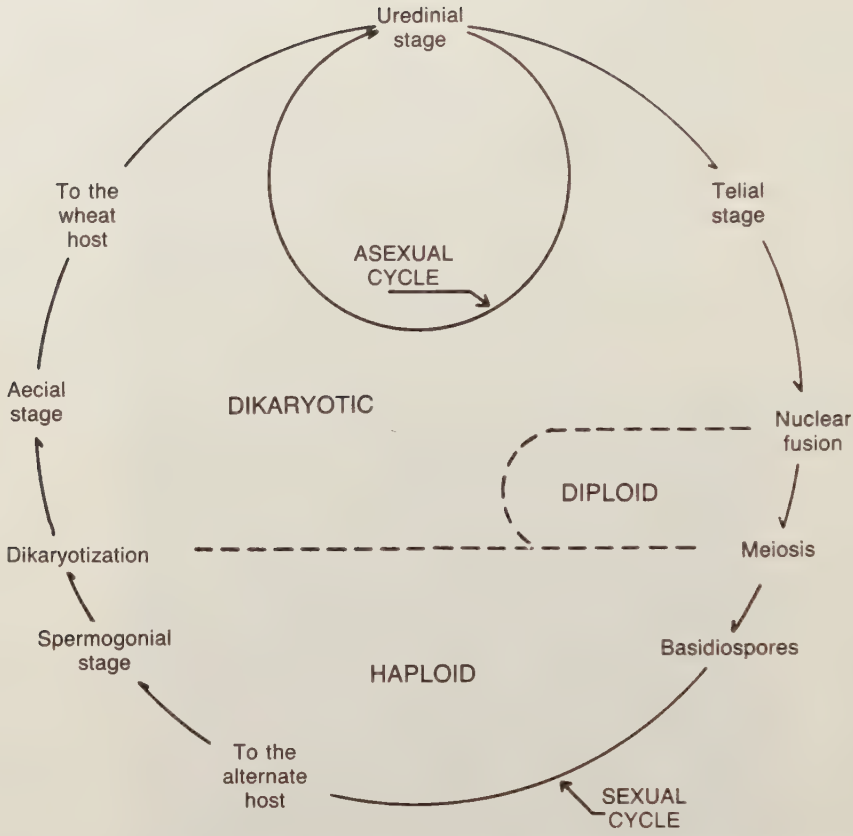

Fig. 8C–5. Complete life cycle of the wheat rust fungi. *Puccinia graminis* and *P. recondita*. Only the wheat host portion is known for *P. striiformis*.

intermountain areas of the Pacific Northwest and the northern Appalachians where *Berberis* spp. can be found. The uredinial, repeating stage is an asexual or clonal cycle, whereas the full telial, basidial, spermogonial, aecial cycle (Fig. 8C–5) provides a sexual stage with its corollary segregation and recombination of genes.

8C–1.2.3 Cytology

The spermatia and hyphae from which they originate were shown to be uninucleate by Sappin-Trouffy in France in 1896 (Schafer et al., 1984). Craigie, in Canada in 1927, demonstrated experimentally for *P. graminis* that these are male gametes and that the spermogonia are thus sexual structures (Schafer et al., 1984). Fertilization of one spermogonium by spermatia from another led to the development of aecia. Allen (1923, 1926, 1928), in cytological studies, described the fusion of spermatia with hyphae from other spermogonia, confirming the cereal rust fungi to be heterothallic and monoecious. Blackman in 1904 had already demon-

strated that binucleate or dikaryotic cells occurred at the base of the aecia, in their development from previously uninucleate hyphae (Schafer et al., 1984). This dikaryotic condition, resulting from spermatial fertilization, remains through aeciospores, urediniospores, and teliospores. Sappin-Trouffy showed that the paired nuclei fuse during maturation of teliospores and that upon their germination to produce basidia, two divisions (one meiotic) occur in the basidia to give rise to the uninucleate basidiospores (Arthur, 1929; Schafer et al., 1984, p. 13–14). The nuclear condition of these fungi is thus 1n (haploid, uninucleate) in the basidiospores, spermogonia, and spermatia; n + n (binucleate or dikaryotic) in aecia and aeciospores, uredinia and urediniospores, and telia and immature teliospores; and 2n (diploid, uninucleate) in mature teliospores, following karyogamy and prior to germination with its meiotic division.

8C–1.3 Pathogenesis

8C–1.3.1 Histology

Classical studies of Allen (1923, 1926, 1928) provided the essential knowledge of the physical relation of the wheat rust fungi to the infected wheat host plants. She showed that infection occurs through stomata. Upon germination of urediniospores on the leaf surface, germ tubes grow laterally across this surface until a stoma is reached. Chemical and physical stimuli on the host surfaces are believed to trigger the development of infection structures (Staples and Macko, 1984). Protoplasm of *P. graminis* and *P. recondita* aggregates at the germ tube tip into an appressorium over one end of a closed stoma. An infection peg is produced, which forces its way through the stoma. *Puccinia striiformis* germ tubes enter stomata directly without obvious appressoria. Upon entering a stoma, the hyphal tips enlarge into substomatal vesicles, from which intercellular hyphae grow. *Puccinia graminis* grows along the under surface of the epidermal cells, whereas *P. recondita* grows inward at a right angle to the epidermis (Allen, 1923, 1926). The intercellular hyphae contact mesophyll cells, into which penetration occurs, with development of intracellular haustoria, the apparent feeding structures of the parasite. During this growth process, protoplasm continues to aggregate at the growing tips of the mycelium and specialized structures, with no apparent external nutrition until haustoria are formed.

Penetration of the host cell wall is followed by an invagination of the host cell plasmalemma, which is not ruptured, forming an interface of this host cellular membrane with the surface of the invading fungal haustorium (Harder and Chong, 1984). Upon haustorial formation, hyphal branches are developed, and the fungus ramifies within the immediate host tissue area, and further haustoria are formed as additional host cells are contacted. The structure of haustoria and their relation to their host cells became amenable to detailed study with the advent of electron microscopy. The classical study is that of Ehrlich and Ehrlich (1963);

reviews are provided by Littlefield and Heath (1979) and Harder and Chong (1984).

After 7 to 10 days of mycelial growth, urediniospores are produced near the center of the infections and rupture the host epidermis, forming a pustule or sorus. Spores are liberated through the open epidermis. New urediniospores continue to develop and emerge as long as a nutritional relation is maintained with host tissue. *Puccinia graminis* produces long, straight runner hyphae in the intercellular spaces that expand the infection and lead to secondary uredinia. *Puccinia recondita*, in contrast, produces secondary uredinia only in a small oval around the primary sorus in extremely susceptible hosts, with limited runner hyphae. *Puccinia striiformis*, in turn, has much more extended runners, largely longitudinal (because of the host internal structure). These develop successive reproductive centers, in a linear orientation, leading to consecutive waves of uredinial formation. This produces long stripelike lesions, constituted from this chain of uredinia rather than the rings of secondary uredinia as found in the other two rust species. As host tissue and infections age, teliospores start to form along the edges of existing uredinia in all three species.

8C–1.3.2 Physiology

Damage to the wheat plant from stem rust results generally from lodging of the weakened straw, poor seed set, and shriveled grain. Johnston (1967) pointed out that significant losses occurring from leaf rust are often overlooked because of the lack of severe grain shriveling and other obvious effects—in contrast to stem rust. Host–parasite relationships can be described on a functional and biochemical basis as well as on the physical interaction. The effects on host tissue have been reviewed by Bushnell (1984); those on plant development as affected by solute distribution have been reviewed by Durbin (1984).

In their obligate parasitism, the wheat rust fungi cause the host cells to change but to continue to live while the parasite develops and reproduces (Bushnell, 1984). There is intense metabolic activity at the infection site on the part of both host and parasite. Host cells show an initial juvenile, antisenescence response to rust infection in which they remain physiologically young. Later on, in contrast, the cytoplasmic organelles slowly disappear and the cells become highly senescent. In the first stage, internal cellular activity concentrates at the site of haustorial invasion. The endoplasmic reticulum network seems to increase, golgi bodies increase in number, and the nucleus, mitochondria, and chloroplasts migrate toward the haustorium. There may be nuclear enlargement, and there is increased synthesis of RNA and cytoplasmic protein. In contrast later, as the rust fungus begins to sporulate, the cytoplasmic organelles degenerate, the endoplasmic reticulum breaks into vesicles, and the nucleus shrinks. Host cells may remain alive 21 to 28 days after infection, but finally the only remaining parts are the host nucleus and fungal haus-

torium (Bushnell, 1984). In short, during the early vegetative stage of infection, the host cells are maintained in an excessively active, juvenile condition, whereas after fungal reproduction the reverse is true, and senescence is accelerated with cell constituents digested and probably utilized by the fungus. The several plant hormones studied generally increase in rusted tissues. They may be the inducers of the successive physiological effects described here. The various physiological activities are similar among the wheat rusts but are most pronounced in stem rust (Allen, 1923).

These results on host cells and tissues also lead to more general effects on the growth and development of the plants. Durbin (1984) noted that the cereal rusts create a major imbalance in the distribution of solutes within the plant. During the normal life history of the plant this distribution is a complex, dynamic process, the later stages of which are dominated by translocation of solutes and nutrients to the developing grain, the plant's reproductive bodies. Rust infections function as competing import regions, or sinks, to which these solutes are directed. This, of course, favors the parasite's reproductive bodies, the urediniospores produced at these localized infection sites. This action disrupts the normal plant physiology and may have manifold effects on various aspects of plant growth and development. Radioactive labeling of solutes showed that they accumulate at infection sites both because of increased movement to these sites and decreased movement away. The fact that cells in infected regions remain in a juvenile condition longer than normal intensifies both of these effects. This accumulation occurs at the expense of other parts of the host plant (Durbin, 1984). Upon the subsequent rupture of the host epidermis following fungal sporulation, there is also a large, localized water loss (Johnston, 1967) that further increases the flow to such regions. Overall water requirements are increased, which may be damaging during times of water stress.

8C–1.4 Epidemiology

Wheat rusts are airborne pathogens that may be disseminated long distances by asexual urediniospores that are produced in great quantity. Saari and Prescott (1985) proposed 10 epidemiological zones for the cereal rusts on a worldwide basis. They define these as regions that have an endemic focus of primary rust infection with free movement and exchange within the region. Within each zone there may be subzones. There may be areas within a zone that require exogenous primary inoculum from other areas within the zone. For example, in the central Great Plains of North America, leaf and stem rust fungi overwinter on winter wheat in the more southerly portion and urediniospores annually blow north to the spring wheat region of the north central USA and adjacent Canada, where overwintering is more rare.

Prior to the barberry eradication program in the USA, the hardy teliospores and the subsequent sexual cycle provided a source of over-

wintering inoculum of stem rust in the north. Since the intensive removal of susceptible barberries in the USA, beginning in 1918 (Roelfs, 1982), stem rust has been largely asexual in nature and totally dependent on the survival of the urediniospore stage somewhere within the epidemiological zone for the full year to complete its total epidemiological cycle, much as leaf and stripe rust are. Both oversummering and overwintering must be accomplished. This requires a greenbridge of some sort between crops (Roelfs, 1986). This may be achieved by the presence of volunteer plants, accessory hosts, or movement between epidemiological subzones.

Each of the wheat rusts has a different set of optimum temperatures, so they may have differing degrees of importance in different areas of the world, at different elevations, and at different times of the year. Stem rust is the warm temperature disease, stripe rust the cool area disease; leaf rust is in between.

Epidemics occur when a susceptible host is present in suitable quantity, with a virulent population of the pathogen, under favorable conditions of the environment, over a suitable period of time. Variations in one or more of these factors lead to the differences among years in rust development and severity. Because of the highly specialized nature of resistance and virulence, a wheat cultivar may be resistant to one population of a rust pathogen and susceptible to another. Conversely, for the same reason, a population of the pathogen may be virulent to one group of cultivars, but avirulent to other cultivars (Roelfs, 1986). In the presence of differentially resistant cultivars, avirulent rust populations will be reduced and the virulent populations selectively increased. Over time this may result in the total replacement by the latter within the natural pathogen population.

Techniques are in the process of development to systematically evaluate the severity and progress of rust epidemics from a distance, through the analysis of reflectance data from the crop through aerial photography, ground-based sensing, or satellite scanning (Sharp et al., 1985).

8C-1.4.1 Stem Rust

Stem rust has been most important in North America on spring wheats because, with their late seasonal development, they are available for infection during a warm period of the year. The almost explosive nature of rust multiplication allows a major epidemic to build up during the relatively short period of the spring wheat life cycle. This led to the devastating epidemics of past years (Roelfs, 1978). Stem rust is much less important in the South because the earliness of crop development, during a cooler period, does not allow enough time of favorable environmental conditions for the rust to become epidemic before crop maturity. However, stem rust can and has occurred in epidemic form on winter wheats in the USA, particularly at the northern edge of production. The degree of infection occurring on winter wheats early in the season can, nevertheless, provide an adequate amount of inoculum for the later,

more vulnerable northern crop for this readily disseminated airborne pathogen. Although overwintering varies by year, it occurs in North America principally south of 34° N Lat (southern Oklahoma) (Roelfs, 1985b). The more recent effective use of broadly based resistance in the spring wheats, along with the prior eradication of barberry, has essentially eliminated stem rust epidemics in the spring wheat region since 1955 (Roelfs, 1978; Green and Campbell, 1979; Schafer and Roelfs, 1985).

8C–1.4.2 Leaf Rust

Leaf rust, although less devastating, is more general in distribution than stem rust because of its tolerance of lower temperatures. It is a major disease of wheat throughout the USA and Canada (Roelfs, 1985b; Samborski, 1985). The fungus can overwinter on winter wheat wherever fall-infected leaves survive until spring. In the central Great Plains, this is common south of 40° N Lat (northern Kansas) and also in the Pacific Northwest (Roelfs, 1985b) and in the East, north into New York (Chester, 1946). In contrast to stem rust, epidemics have been more frequent in the winter wheat regions of the USA. In recent years the most severe disease occurrence has been in the South and Pacific Northwest (D.L. Long, Cereal Rust Laboratory, 1986, personal communication), because of the relatively effective use of resistance in other areas.

8C–1.4.3 Stripe Rust

Stripe rust is most epidemic in cool, wet climates. It is the most important wheat rust disease of northwestern Europe; it also occurs on wheat grown at higher altitudes around the world. In the USA it occurs mainly in the Pacific Northwest, although in unusual years it has been found early in the season on winter wheat in the southern Great Plains. In the Pacific Northwest it is endemic on the wheat crop or on green-bridging plants throughout the year (Hendrix, 1967). Coakley et al. (1983) studied long-term disease and weather data showing that stripe rust was most severe in seasons following mild (warmer than average) winters (favoring overwintering) but with cooler than average springs (favoring disease development). Statistical models for predicting the potential severity of stipe rust have been developed from these data.

8C–1.5 Control

Any factor that breaks the disease cycle of the wheat rust fungi or reduces the magnitude of any part of the cycle acts as a control measure. This can be brought about by a variety of means. Possible control measures include escape, either because of early cultivar maturity or by varying the planting date; reduction in oversummering or overwintering of the pathogen; removal of an alternate host; appropriate utilization of host–plant resistance; application of antiseptic or therapeutic chemicals;

and, conceivably, some sort of biological control measure (although practical biological controls have not yet been developed). For the cereal rusts in North America, host–plant resistance is the primary means used. Usually, a combination of control efforts is advantageous.

8C–1.5.1 Disease Escape

This approach to rust control reduces the period of time over which the crop is exposed to the pathogen under favorable conditions. This aims to lessen the period of disease development and at its extreme would lead to total escape from disease. The cereal rusts are diseases which increase logarithmically (Vanderplank, 1963). Multiplication of propagules in each infection cycle may be several orders of magnitude, so that each cycle may cause more disease in a location than all previous cycles combined. In such a system, any shortening of the available period for disease will greatly reduce the final amount of disease and resulting loss. Production of cultivars maturing earlier than those grown previously, beginning with Triumph in the Hard Red Winter Wheat Region (Briggle and Reitz, 1963) and Knox in the Soft Red Winter Wheat Region (Caldwell et al., 1954) of the USA, considerably reduced the time available for buildup of stem rust in these regions and improved the chance for escape from disease. Reduction of rust on winter wheats in turn reduces the inoculum available to move north to the spring wheats in the North American Wheat Belt.

Early spring planting of spring wheats may also lead to early maturing and lessened favorable exposure when compared to a later planting date. In contrast, late fall planting of winter wheat may provide a shorter time for fall buildup of inoculum prior to the advent of the winter period, and may provide a longer gap from the previous harvest, breaking the greenbridge. This delayed planting is limited by the need to establish plants before the winter, and each region will have its optimum compromise. Other diseases and pests will also be factors. In some U.S. winter wheat areas this optimum late planting date is similar to the Hessian fly-free date.

8C–1.5.2 Reduction of Oversummering

Obligate parasites such as the cereal rust fungi need a greenbridge of some sort throughout the year. This is most evident during the time from harvest to fall planting, the period of oversummering in winter wheat areas. In the central Great Plains of the USA, crop cultural recommendations frequently include the destruction of volunteer wheat during this intercrop period. This is mainly recommended for the control of wheat streak mosaic, but also provides for removal of leaf and stem rust inoculum. Such volunteer plants are believed to be a major source of inoculum between wheat crops in the Cone region of South America (A.P. Roelfs, Cereal Rust Laboratory, 1982, personal communication). Zadoks

and Bouwman (1985) reported this also for stripe rust in northwestern Europe.

Mehta observed in India in 1940 that cereal rusts could not oversummer in the Indo-Gangetic Plain and must be renewed each year from cooler areas (Nagarajan and Joshi, 1985). Legislation to suspend wheat cultivation in these other areas was attempted for a period but is not now considered to have been effective (Nagarajan and Joshi, 1985).

8C-1.5.3 Reduction and Monitoring of Overwintering

Direct limitation of overwintering of rust within the wheat crop has not generally been considered practicable. However, regulatory banning of winter barley in Denmark and parts of the Netherlands has been enforced to protect the more important spring barley crop from both stripe and leaf rust (Zadoks and Bouwman, 1985). This is considered to have been effective, as a result of the reduced amount of initial endemic inoculum for the spring crop.

Monitoring of the overwintering, rather than its direct control, with resultant prediction of an epidemic and possible subsequent chemical control has also been utilized. The pioneer in this was Chester (1946, p. 151), who developed his "critical month" concept in the determination of the amount of overwintering of leaf rust in Oklahoma. Coakley et al. (1983) developed statistical models for predicting stripe rust on winter wheat in the Pacific Northwest, using only meteorological data. This information, in combination with rust data, allowed Line (1983) to recommend effective chemical control of a potential stripe and leaf rust epidemic in the northwestern USA in 1981.

8C-1.5.4 Alternate Host Eradication

By careful inoculation experiments, de Bary in Germany conclusively proved in 1866–1887 that infection of barberry occurred from basidiospores developed from teliospores of *P. graminis* from wheat, and in turn that infection of wheat occurred from aeciospores from barberry (Schafer et al., 1984). Previously in 1806, Knight had infected wheat from rusted barberry (Hermansen, 1968). The stem rust relation between barberry and cereals already had been generally recognized by farmers much earlier, as demonstrated by a barberry eradication law enacted in Rouen, France, in 1660 (Fulling, 1943; Roelfs, 1982). Similar laws were subsequently passed in other European countries and in the American colonies over the next two centuries. The barberry controversy in Denmark extended from 1805 to 1865 (Hermansen, 1968). A strengthened law in 1904 led to the nearly complete eradication of barberry in Denmark (Stakman, 1923). Following the severe epidemic of stem rust in North America in 1916, an extensive barberry eradication effort was mounted (Roelfs, 1982). This program achieved its major success by 1927, and most efforts in the USA were terminated by 1980. Roelfs (1982) concluded that four main beneficial effects on the frequency and severity of stem

rust epidemics in the North American spring wheat region were achieved by eradication of barberries: delaying disease onset by about 10 days, reducing initial inoculum, decreasing the number of pathogenic races, and stabilizing the pathogenic races. The latter two factors result from the elimination of sexual recombination in the life cycle of *P. graminis*, and the others, of course, from the removal of early inoculum.

8C-1.5.5 Utilization of Host-Plant Resistance

Stem rust was very early recognized as a severe problem of wheat in Australia. Cobb (1890) began a study of resistance, and Farrer (1898) included resistance as a breeding objective about 1890 (Schafer, 1974). Biffen (1905) in England first applied Mendelian genetics in a study of stripe rust resistance (Schafer et al., 1984). Breeding for stem rust resistance in the USA began in Minnesota and Kansas, in cooperation with the U.S. Department of Agriculture, immediately after the severe 1904 epidemic. 'Kanred' winter wheat and 'Ceres' spring wheat were early releases from these efforts, but very shortly both succumbed to the presence of new races of the pathogen, which had the capacity to overcome their resistance characteristics, or conversely, to which these resistances were not effective. These wheat cultivars were thus differentially resistant to various parts of the pathogen populations and provided a selective screen for those elements to which they were susceptible and eliminated that portion to which they were resistant. This led to a change in the rust races and the loss of effectiveness of the resistance of such cultivars. It was in this agricultural evolutionary process that such pathogenically different races of the rust fungi were first identified for wheat stem rust by Stakman and Piemeisel (1917). This phenomenon presented a very different and much more complex picture of breeding for rust resistance, and forced a reevaluation of the strategies for effectively using resistance that is still going on. Present concepts include the utilization of general or race-nonspecific resistance, use of tolerance to the pathogens, and various means of deployment of race-specific resistance. The goal is to generate a durable resistance. This concept was reviewed by Johnson (1984).

8C-1.5.5.1 Race-Specific Resistance. Following the comprehension of the ephemeral effectiveness of many sources of wheat rust resistance, efforts were begun to devise schemes to increase the functional life of such resistance. Proposals have included sequential use of different resistance genes over time, interregional diversity, interfield diversity, intrafield diversity, and the genetic combination of different genes for resistance (Schafer, 1974). Sequential use of resistance genes one at a time is not currently actively proposed, as the effective life of many such genes is so short. This appears to be particularly true for stripe rust. However, in historic practice this nonstrategy was the initial strategy.

Interregional diversity of resistance in the USA is represented by the use of the Triumph cultivar and its successor cultivars, possessing the

Tmp gene, in the Hard Red Winter wheat region (McVey and Hamilton, 1985). This provides resistance to all North American stem rust races except races 15 and 56, to which in turn different genes provide resistance in the Hard Red Spring wheats. Along with the early maturity of Triumph, this different resistance in the central Great Plains appears to have been an important factor in the long-term effectiveness of stem rust resistance in North American Hard Red Spring wheats to the north.

Interfield diversity may be provided by the use of different sources of resistance in cultivars developed for a given area. When such cultivars are available, diversity may occur through farmers' random choice. Parlevliet (1981) pointed out that experience shows this usually to be inadequate, however, in hindering the development of virulent races. In the United Kingdom, available cultivars are classified annually as to their stripe rust resistance so that farmers can systematically choose those of differing resistance to provide diversity on their farms (Doodson, 1982)

Intrafield diversity is represented by the use of multilines or cultivar mixtures. Browning and Frey (1969) pioneered this proposal for oats, and a stripe rust resistant wheat multiline, Crew, was released in the Pacific Northwest (Allan et al., 1983). Multilines provide excellent protection from rust (Mundt and Browning, 1985). However, their durability over time in comparison to other strategies for deployment of specific resistance genes has not yet been well tested on a commercial scale. The theoretical basis for their possible durability has been explored by Groth (1976).

Genetic combination of resistance genes into a single cultivar was first proposed by Watson and Singh (1952) for use in rust control in Australian wheat as a means of piling up several genetic barriers to the selection of pathogenic races of the rust pathogens. This approach is often called *pyramiding* or *stacking* of resistance genes. This appears to be the primary basis of the effectiveness of the resistance to stem rust in North American spring wheats that has lasted for 30 yr (into the 1980s) (Green and Campbell, 1979; Dyck and Kerber, 1985). To overcome such resistance the fungus must develop virulence at each pathogenicity locus corresponding to the resistance genes of the cultivar. This must occur either simultaneously or sequentially. The statistical possibility of this occurring simultaneously for very many resistance genes appears greatly reduced compared to the occurrence of single-gene variations (Schafer and Roelfs, 1985). Sequential occurrence requires the presence and buildup of intermediate populations.

Numerous genes for specific resistance to each of the wheat rusts have been identified and tabulated. These are listed in the Catalogue of Gene Symbols for Wheat, periodically issued by McIntosh (1983) (see also sections 4G and 4H, above). Specific genes for stem rust resistance (Roelfs and McVey, 1979; Luig, 1983), leaf rust resistance (Browder, 1980), and stripe rust resistance (Robbelen and Sharp, 1978) are listed, characterized, and discussed in detail. See Dyck and Kerber (1985) for a

discussion of cereal rust resistance of the race-specific type. Browder (1971) discussed the concepts of the complementary specialization of the rust fungi to these resistances and detailed methods of study for this.

8C-1.5.5.2 Race-Nonspecific Resistance. With the loss of effectiveness of some resistance, as a result of shifts in the pathogen populations, it became evident that other, often lower degrees of resistance were not so easily nullified and appeared to be more durable in their effects (Parlevliet, 1985).

Parlevliet (1985) showed that apparent race-nonspecific resistance can result from the fact that the incremental differences (effects of individual genes) may be so small that they cannot be distinguished from various facets of experimental error. Nonspecificity can also result from a real lack of cultivar–race interaction. These two phenomena, if both exist, are difficult or nearly impossible to distinguish. Although race-nonspecific resistance is not polygenic by definition, it appears in practice, largely to be so, and thus may be the cumulative effect of several or numerous genes. Sharp and associates (Lewellen et al., 1967) intensively studied this type of resistance for stripe rust, Shaner (1980) and associates (Lee and Shaner, 1985a, 1985b; Ohm and Shaner, 1976; Shaner and Hess, 1978) for leaf rust, and Wilcoxson (1981) for stem rust in the USA. This resistance has been found to result largely from the occurrence of fewer pustules (receptivity), a longer period of time to sporulation (longer latent period), and lesser spore production (Ohm and Shaner, 1976; Parlevliet, 1985). These individually or collectively, lessen disease and result in slow rusting. Some studies show this resistance to be independent of race-specific resistance (Parlevliet, 1985) and in other cases it is associated (Rowell, 1982). Race-nonspecific resistance appears to be relatively durable on the basis of experience, but the data on this are scant. Equations were developed to predict how components of slow rusting interact in field epidemics. These show which resistance components are most effective in slowing an epidemic and what magnitude of each component is optimum, and point to applications to breeding for resistance (Shaner and Hess, 1978; Shaner, 1980). Genetic control of differences in latent period was found often to be by two or three partially recessive genes, which differ in different cultivars and are combinable into even slower rusting types (Lee and Shaner, 1985a and 1985b).

8C-1.5.5.3 Tolerance. Another form of resistance, as broadly defined, is tolerance. Cobb (1894) wrote that "some plants have a power to endure rust." Several definitions have been provided (Schafer, 1971). A useful direct one is that of Simons (1969), indicating that a tolerant cultivar shows signs and symptoms similar to those on a susceptible cultivar but is less damaged by infection. Roberts et al. (1984) reported the occurrence of tolerance to leaf rust of potential economic importance, but no promising breeding methods are presently available. The lack of selective pressure on the reproductive capacity of the pathogen makes

tolerance more stable than some other resistance; however, because disease is fully expressed, tolerance is unlikely to provide major protection (Schafer, 1971). Concepts of plant disease tolerance have been reviewed by Schafer (1971) and more recently by Gaunt (1981).

8C–1.5.6 Chemical Control

Intensive cropping and high potential yields of wheat in Western Europe have provided for an economic use of chemical control for the rusts (Rowell, 1985). In contrast, the extensive cropping on less productive land in North America has not encouraged chemical control. Following the 1953–1954 wheat stem rust epidemics and a loss of confidence in resistance, there was a surge of interest in the development of effective chemicals for control of wheat rusts. Rowell (1985) reported that not only was effectiveness required, but such chemical materials must also meet toxicological and economic requirements. Several chemicals that were highly effective in controlling wheat rusts were not suitable either because of phytotoxicity to the wheat, the presence of toxic residues in the grain, or excessive costs that made their use not economical. The effectiveness of rust resistance in most areas much of the time in recent years also has deterred use of fungicides. However, chemical applications were very effective in providing economic control of leaf rust in northwestern Mexico in 1977 (Dubin and Torres, 1981) and of stripe and leaf rust in the Pacific Northwest of the USA in 1981 (Line, 1982) in the face of incipient severe epidemics. In both cases this use was allied with disease prediction systems (Dubin and Torres, 1981; Coakley et al., 1983), which determined that the potential level of loss was so great as to make the fungicide applications economical. The control was possible because after many years of research and development there are now available effective, systemic, nonphytotoxic rust-controlling fungicides (Rowell, 1981). Use of chemicals appears best as an integrated measure with some degree of host–plant resistance, and coordinated with appropriate disease forecasting (Rowell, 1985). However, a fungicide must be applied relatively early in the development of an epidemic to provide economical control, although this varies with the properties of the fungicide (Rowell, 1985).

8C–2 WHEAT SMUTS

The smuts were among the first diseases of wheat to be investigated, with an important study by Tillet (1755) in France. The economic control of common bunt, one of the smuts that was once a devastating disease worldwide, primarily by chemical seed treatment and supported by the use of resistance, is one of the major success stories of plant disease control (Hoffmann, 1982).

8C–2.1 Diseases

There are four distinctly different smut diseases of wheat: bunt or stinking smut, loose smut, flag smut, and Karnal or partial bunt (Holton, 1967). These are conspicuous, damaging diseases, three of which directly affect the kernels or spikes of the plants. Bunt is further separated into common and dwarf bunt, which are caused by different pathogen species and differ in symptoms, disease cycle, and environmental requirements, and will be considered separately here. Common bunt, in turn, is caused by two related fungal species, inciting essentially the same disease (Holton, 1967; Wiese, 1977).

8C–2.1.1 Descriptions

8C–2.1.1.1 Common Bunt. The bunts are characterized by the replacement of the normal kernel by a sorus, called a *bunt ball*, composed of fungal spores enclosed in the host pericarp (Fig. 8C–6). Diseased plants may be slightly stunted. Infected heads are usually more slender (Fig. 8C–7), and glumes may be abnormally spread apart by the enclosed bunt ball. Bunt balls are more nearly spherical than wheat kernels, and are

Fig. 8C–6. Bunt balls (*upper*) mixed with normal wheat kernels. (Photo by the Illinois Agric. Exp. Stn., from M.V. Wiese, 1977, *Compendium of Wheat Diseases*. Reprinted by permission of the American Phytopathological Society, St. Paul.)

Fig. 8C–7. Bunt-infected wheat spikes (*center*) with normal spikes (*outside*). Two spikes on left are common wheat and two on right are club wheat.

Fig. 8C–8. Combine in bunt-infected wheat field in Pacific Northwest prior to major control of this disease in the 1950s. This shows the high degree of infection and the massive infestation of soil, equipment and grain.

fragile. They often rupture upon threshing, releasing the black, powdery fungal spores into the air as a black cloud (Fig. 8C–8) to contaminate the grain and soil. Usually entire plants and spikes are infected, but not always. The spores have a fishy odor, evident in infested grain and even noticeable in standing wheat that has a high incidence of disease; this is due to a volatile material, trimethylamine.

8C–2.1.1.2 Dwarf Bunt. Symptoms are similar to those of common bunt except for the additional characteristic of extreme dwarfing of

infected plants (Fig. 8C–9). However, the spikes are usually broader than normal or than those with common bunt (Trione, 1982). Infected plants tiller more profusely, and partial plant and spike infection is more likely than with common bunt. Dwarf bunt was first identified as a distinctly different disease from common bunt by P.A. Young in 1935 (Conners, 1954).

8C–2.1.1.3 Karnal Bunt. In contrast to common bunt, this disease is characterized by a partial infection of plants and kernels. The sorus containing the fungal spores replaces a variable portion of the kernel, usually along the longitudinal furrow and into the endosperm and scutellum (Fig. 8C–10). The odor of trimethylamine is also present (Joshi et al., 1983).

8C–2.1.1.4 Loose Smut. Symptoms are striking in that the entire spike is usually replaced by the fungal spores, initially enclosed in a fragile membrane that soon ruptures. This leaves a powdery black spore-laden diseased head (Fig 8C–11). Spores are easily removed by wind and rain, eventually leaving the bare rachis (Wiese, 1977). In severely ramified infections, sporulation may rarely also occur in leaf tips.

Fig. 8C–9. Noninfected wheat plant (*left*), common bunt-infected (*center*), and dwarf bunt (*right*).

Fig. 8C–10. Varying degrees of Karnal bunt infection of wheat kernels. (Photo courtesy of L.M. Joshi, D.V. Singh, K.D. Srivastava, and R.D. Wilcoxson.)

8C–2.1.1.5 Flag Smut. This disease is unique among the wheat smuts in producing extensive linear sori on the leaves and culms (Fig. 8C–12) (Purdy, 1965; Wiese, 1987). There is also a general stunting and distortion of plants. Severely infected plants may not develop heads at all.

8C–2.1.2 Early History

Tillet (1755) in France provided the first scientific study of the wheat smut diseases. He clearly distinguished smutted (loose smut) from bunted wheat on the basis of symptoms. His experiments led him to propose that bunt was contagious and that the source of the contagion was the black dust (spores) in the bunt balls. He further identified certain seed treatments to reduce the amount of disease. Also in France, Prevost (1807) further described the bunt disease and its development in great detail. He germinated spores and attributed them to a microscopic plant that he considered to be the cause of the disease. Keitt identified this as the first experimental demonstration of the role of a microorganism in the causation of disease (preface to Prevost, 1807). Voluminous and thorough early studies of the smut fungi as a related group were those of Oscar Brefeld in Germany between 1877 and 1912 (Fischer and Holton, 1957).

Common bunt is worldwide in distribution and very early was believed to be the most serious disease of wheat in many areas. In 1890 bunt was estimated to destroy one-fourth to one-half of the wheat crop of Kansas, and in the Pacific Northwest for many decades it was by far the most destructive disease of wheat (Holton and Heald, 1941).

Fig. 8C–11. Loose smut infection, compared to healthy wheat head (*left*). Bare rachis following blowing and washing away of teliospores from infected spike (*right*). (Photo by E.D. Hansing, from M.V. Wiese 1977, *Compendium of Wheat Diseases*. Reprinted by permission of the American Phytopathological Society, St. Paul.)

A unique early sidelight to the presence of bunt was the occurrence of dust explosions in wheat-threshing machinery, caused by the extremely large volume of spores, along with other carbonaceous dust, in an infected crop (Cardiff et al., 1914; Fischer and Holton, 1957). The equipment, grain, and personal injury losses became so acute that special attachments were installed on threshing equipment to prevent the explosions (Holton and Heald, 1941; Fischer and Holton, 1957).

Seed treatment was very early brought to bear on the seedling infecting smuts. Salt brine was used about a century before the scientific research of Tillet (Fischer and Holton, 1957). Over the years a wide array of materials has been used, including Cu compounds, HCHO, Hg compounds, and later various organic chemicals.

Being internal in the seeds, loose smut infections long resisted chemical treatment. This problem was imaginatively solved by a Danish seedsman, Jensen (1888), through a hot water treatment of seed. This technique works because the wheat embryo can withstand a higher temperature than the internal mycelium of the infecting loose smut fungus (Fischer and Holton, 1957). Although difficult of application and tedious, it remained a valuable technique until the advent of systemic chemical fungicides.

Fig. 8C–12. Flag smut of wheat.

8C-2.1.3 Crop Production Limitation

Tillet (1755) considered diseases that destroyed the complete wheat head or entirely replaced kernels to cause the greatest losses, thus including both bunt and loose smut as two of his three further subdivisions of diseases which he considered to cause the major loss to wheat production in France in the mid-18th century.

8C-2.1.3.1 Common Bunt. Historically, bunt has been the most destructive of the wheat smuts in the USA (Fischer and Holton, 1957; Holton, 1967). The severe losses of earlier times in the central and eastern USA were fairly quickly reduced by use of seed treatment. In the Pacific Northwest the bunt problem was much more persistent because the fungus is soilborne as well as seedborne in this less humid region and was less amenable to control by seed treatment. Since the mid-1950s, beginning with the use of hexachlorobenzene seed treatment, common bunt has been reduced to insignificance in the Pacific Northwest as well as

throughout all of the agriculturally developed areas of the world (Hoffmann, 1982). Serious losses continue, however, in less-developed regions. Hoffmann (1982) reported a 5 to 7% annual loss from common bunt in North Africa and central Asia as recently as 1979, with this disease being second only to the rusts in importance in these areas. Common bunt not only reduces yield, but the contamination of the grain by the spores also reduces quality for milling or feed. United States official grain standards provide for a special grade of smutty wheat and for smut dockage designations, which substantially reduce the market value of the grain.

8C-2.1.3.2 Dwarf Bunt. The nature of losses from dwarf bunt is the same as for common bunt, but the disease is much less widespread. The more limited geographic range of the disease and its tenacious resistance to control have, however, led to quarantines against regions in which it occurs. China has a zero tolerance for dwarf bunt in wheat and since 1974 has not accepted wheat from the U.S. Pacific Northwest states (Trione, 1982). As China is currently a major wheat importer, this has been a significant loss to this region, which exports 85% of its wheat.

8C-2.1.3.3 Karnal Bunt. In contrast to the widespread occurrence and historic losses from common bunt, Karnal bunt is a minor disease. Joshi et al. (1983) reported that even in years when epidemics were most severe, damage to India's total wheat crop was $< 0.5\%$, although occasional fields had nearly 90% infected kernels. Milling quality and seed viability are both reduced.

8C-2.1.3.4 Loose Smut. Loose smut occurs wherever wheat is grown but at a higher incidence in humid regions (Martens et al., 1984). Prior to the development of systemic fungicides, losses remained consistent from year to year at a relatively low but significant level, reported at 0.8% for the USA during the 1950s (LeClerg et al., 1965). Losses as of 1986 have been considerably reduced, but the disease has not disappeared.

8C-2.1.3.5 Flag Smut. In the USA, flag smut is currently found in more than trace amounts only in two dryland counties of Washington and Oregon (Purdy, 1965), and does not occur in Canada (Martens et al., 1984). It occurs in various arid wheat-producing regions of the world, particularly the Middle East and Australia (Purdy, 1965), where it has at times been considered a serious threat. Overall losses in North America are negligible.

8C-2.2 Pathogens

8C-2.2.1 Taxonomy

The pathogens causing the smut diseases of wheat are members of the fungus order Ustilaginales, which is synonomous with the term smut fungi. This is divided into two familes which in turn consist of 35 genera

and about 1100 species (Duran, 1973). The six species attacking wheat are found in three or four genera, depending upon classification preference.

8C-2.2.1.1 Common Bunt. This disease is caused by two closely related species, *Tilletia caries* (DC.) Tul. and *T. foetida* (Wallr.) Liro. These parasitize one or more species of *Triticum, Secale, Aegilops, Agropyron*, and *Elymus*. Sori occur in host ovaries. Teliospores of *T. caries* are generally globose with a reticulate surface and 17 to 25 μm in diameter. Those of *T. foetida* are slightly smaller and differ also by possessing a smooth surface (Duran and Fischer, 1961). The life cycles appear identical, and the two species readily hybridize in culture (Flor, 1932) and in nature.

8C-2.2.1.2 Dwarf Bunt. Dwarf bunt is caused by *Tilletia controversa* Kuhn. The spores are nearly identical to those of *T. caries* (Duran and Fischer, 1961) except that the reticulations are wider and deeper and are enclosed in a prominent sheath (Conners, 1954). The biological differences demonstrated by the two diseases were recognized prior to the accepted species separation. Symptom expression also is important in identification, and no single character except teliospore germination requirements is distinctive enough to provide positive identification (Purdy et al., 1963).

8C-2.2.1.3 Karnal Bunt. The fungus causing Karnal bunt is designated as *Tilletia indica* Mitra by Duran and Fischer (1961) in their monograph on the genus *Tilletia*, but as *Neovossia indica* (Mitra) Mundkur by most Indian researchers (Krishna and Singh, 1982; Joshi et al., 1983). *Triticum* and triticale have been reported as hosts. Sori are in the ovaries with only partial colonization occurring. Teliospores are globose, variable in size, but generally much larger (22–49 μm) than those of the common and dwarf bunt fungi (Joshi et al., 1983). The exospore surface is typically composed of truncate projections.

8C-2.2.1.4 Loose Smut. The commonly used species name is *Ustilago tritici* (Pers.) Rostr., designating the loose smut fungus attacking wheat (Nielsen, 1972; Wiese, 1977). This has been consolidated with the form attacking barley as *U. nuda* (Jens.) Rostr. by several authors (Fischer, 1953) but maintained separately in studies of Nielsen (1972, 1978). Sori are in the spikelets, are naked and dusty, and often entirely destroy the floral parts (Fischer, 1953; Nielsen, 1978). Teliospores are globose, with a minutely echinulate surface. They are about one-third the size of those of the common bunt fungi. Although historically known as a specialized pathogen of wheat, *U. tritici* has been successfully inoculated into species of seven grass genera (Nielsen, 1978).

8C-2.2.1.5 Flag Smut. The cause of flag smut is *Urocystis agropyri* (Preuss) Schroet. (Fischer, 1953). It sometimes has been separated into a host-specialized species, attacking only wheat, and designated *U. tritici*

Korn. (Purdy, 1965). The specialized form on wheat has been found in nature only on *Triticum* (Purdy, 1965). *Urocystis agropyri*, as an expanded species, attacks several graminaceous hosts. Sori occur as short to long striations on blades, sheaths, and the rachis of modified spikes. Plant growth is stunted, distortion may occur, and often the head is aborted. Teliospores occur in balls of one to six spores surrounded by smaller, lighter, sterile cells (Fischer, 1953).

8C-2.2.2 Life Cycles

The smut fungi have a less complex life cycle than the cereal rust fungi. They produce teliospores which in turn germinate to form basidia and basidiospores, or, as in *U. tritici*, elongated germ tubes in which the basidial cells fuse without basidiospores. Infection of the wheat plant occurs from fused basidiospores or germ tubes from the germinating teliospores, and leads directly to the next teliospore generation. There is no asexual parasitic cycle, and the sexual process occurs each cycle of infection of wheat. This is in major contrast to the present asexual cycle of infection for the wheat rusts in North America. The only asexual spore stage is the vegetative reproduction and multiplication of basidiospores in the soil or upon artificial culture. Physical stages of the life cycles of the several wheat-infecting smut fungi are essentially the same, but the disease cycles differ widely in the stages of wheat development at which infection and sporulation occur.

In common bunt, teliospores replace the normal kernel in the bunt ball. With the shattering of these at threshing, both seed and soil become infested (Fig. 8C–8). In either case teliospore germination occurs with seed germination, and infection occurs through the coleoptile of the young seedling prior to emergence (Fischer and Holton, 1957). The fungal mycelium becomes seated in the terminal meristem and moves with it as a systemic infection during the growth and development of the wheat plant. This vegetative fungal tissue ramifies throughout the developing ovary and subsequently separates into the thick-walled, single-celled teliospores as the replaced ovary, now the bunt ball, matures.

The disease cycle of flag smut is similar to that of common bunt, except that sporulation occurs earlier in the development of the wheat plant (Purdy, 1965). Fungal ramification from the meristem and subsequent spore development occur in the maturing leaf and culm tissue as linear stripes rather than delaying to the development of the ovary at flowering. The sori are broken up at harvest, and soil and grain are infested preliminary to the next cycle of pre-emergence seedling infection.

The disease cycle of dwarf bunt differs from that of common bunt in the time and point of infection. Spore germination temperature requirements are lower (Lowther, 1948) and the incubation period is longer. Infection occurs in the tiller initials in the crowns of emerged wheat plants in midwinter, rather than in the coleoptile of young seedlings (Purdy, et

al., 1963). This greatly reduces the importance of seedborne inoculum and pinpoints soilborne spores as the major source of infection (Hoffmann, 1982). Systemic infection and sporulation characteristics are the same as for common bunt.

The disease cycle of loose smut differs in that the teliospores are exposed almost immediately after emergence of the infected wheat spikes and are quickly disseminated by wind and rain. The point of infection is through the ovary walls of nearby healthy spikes at flowering time. As the young newly infected seeds develop, the fungal mycelium ramifies in the scutellum of the embryo, where it becomes dormant at seed maturity (Fischer and Holton, 1957). In contrast to common bunt where seeds are externally infested, these seeds are now internally infected by the loose smut fungus. As the infected seeds germinate the fungal mycelium grows with the terminal meristem, becoming systemic in the plant, and ramifying and cleaving into teliospores as the spike develops.

The Karnal bunt disease cycle has differences from and similarities to both common bunt and loose smut. Like common bunt, sporulation occurs in the kernels, from which teliospores infest both seed and soil. Spore germination does not occur with seed germination, however, but is delayed until heading of the subsequent growing crop. Basidiospores and secondary sporidia are produced at the soil surface and carried by air currents or splashing rain to the emerging spikes. Infection leads directly to fungal ramification and immediate sporulation in the currently developing kernels, rather than becoming latent in normal-appearing kernels as in loose smut (Joshi et al., 1983). Infection is local but may spread between florets and spikelets (Gill et al., 1983).

This group of fungi has translated a simple, relatively uniform life cycle into a series of successively varying disease cycles as they relate to the stages of the host wheat plant. This has further led to a series of differing epidemiological patterns.

8C-2.2.3 Cytology

Like the rust fungi, the smut fungi have three nuclear phases (Fischer and Holton, 1957; Joshi et al., 1983). Mature teliospores are diploid (2n). Meiosis occurs at spore germination, leading to a haploid condition (1n) of the basidial cells and basidiospores. The haploid stage can grow saprophytically and under artificial cultural conditions may proliferate and be maintained indefinitely in culture. However, in nature it is normally a short-lived phase, followed shortly by fusion of basidial cells or basidia to initiate a dikaryophase of n + n nuclear condition. The dikaryophase is the normal parasitic, mycelial stage and persists throughout infection until maturity of teliospores, when nuclear fusion occurs to initiate the 2n condition. Details of the occurrences of nuclear stages vary with the smut species, but the overall cycles are similar.

8C–2.3 Pathogenesis

8C–2.3.1 Histology

The smut fungi penetrate directly through the epidermis (Purdy, 1965). This penetration, depending on location and subsequent development, leads to four categories of infection: (i) seedling infection, through the coleoptile (common bunt, flag smut); (ii) shoot infection of vegetative plants (dwarf bunt); (iii) embryo infection, through the ovary wall (loose smut); and (iv) local infection, through the young floral parts (Karnal bunt) (Fischer and Holton, 1957). Following penetration, the mycelium may be both intra- and intercellular (Batts, 1955; Fernandez et al., 1978; Purdy, 1965). It ramifies locally in the case of Karnal bunt (Joshi et al., 1983), proceeds to the developing embryo in the case of loose smut (Batts, 1955), to the lateral meristems for flag smut, ramifying through much of the host tissue (Purdy, 1965), and to the terminal meristem for common and dwarf bunts (Wiese, 1977). As the site and time of sporulation are approached, the mycelium proliferates and aggregates into a dense mass. The cells of this mass subsequently round up (Purdy, 1965), cleave into teliospores and associated cells, and develop the characteristic teliospore walls. This development of teliospores supplies the stage which provides symptom and sign occurrence and location.

8C–2.3.2 Physiology

The mycelium of the smut fungi characteristically aggregates in a specific organ or tissue of the host plant as teliospore development is initiated (Fischer and Holton, 1957). In flag smut this is in stripes in the leaves which lead to their disruption; in the bunts the infected kernels are wholly or partially replaced; and in loose smut the total floral tissue except for the rachis is replaced. In that the heads are often aborted or greatly reduced in flag smut, all of these fungi directly subvert the normal plant resources from the plant's reproduction to their own.

Various secondary effects also occur. Bunt-infected club wheats show a spike modification, in that they are long and lax, appearing much like the spikes of common wheat (Fischer and Holton, 1957) (Fig. 8C–7).

The most obvious gross effect is that of shortening of internodes or dwarfing, most extreme in the case of dwarf bunt. Dwarf bunt also stimulates excessive shoot production, leading to an increased number of tillers.

8C–2.4 Epidemiology

Although the smut and rust fungi are closely related groups, their epidemiological characteristics are very different. The smuts are essentially seed- and soilborne diseases, with only limited, localized airborne aspects in the cases of loose smut and Karnal bunt. The smuts have only one infection cycle per crop cycle, and so are classified as *simple interest*

diseases. Those with a functional soilborne phase (all except loose smut) may become endemic and remain over time in infested areas where the soil environment is favorable.

Common bunt and flag smut have both seedborne and soilborne phases. Contamination of seed with teliospores allows these fungi to be carried to wherever infested seed is moved. Common bunt is worldwide in distribution. Flag smut, with stricter environmental limitations, is less widely distributed and has, in turn, been a target of quarantines. Soilborne phases of both diseases are limited to more arid regions, and in the case of common bunt is not fully extant with the distribution of the disease. Both diseases are endemic where soilborne.

Teliospores of dwarf bunt may also heavily infest the seed, and thus conceivably could disseminate the disease through seed. However, in the absence of infection of seedlings, the seedborne phase appears unimportant. Perpetuation of the disease is dependent upon soil infestation. This in turn is limited to those parts of the world which have a favorable winter infection climate. This is largely at high elevations, with a long period of snow cover and resultant long period of uniform temperature near freezing at the soil surface. This is a disease only of fall-sown wheat. These epidemiological characteristics make dwarf bunt a more localized and sporadic disease than common bunt, but also more difficult to control in its special niche.

Karnal bunt has seed-, soil-, and airborne phases. Seed contamination is a means of transporting the disease and initially infesting the soil, where the sporidia leading to infection arise. For this reason, discovery of Karnal bunt in Mexico, in addition to its long-term Asiatic base, led to the recent U.S. quarantine against wheat from infested areas. The airborne phase transfers sporidia from the soil surface to the wheat spikes. This phase is local and transient, but is essential to the perpetuation of the disease.

Loose smut has only seed- and airborne phases. It thus fills a very restricted ecological niche, but has been able to perpetuate itself over time at a relatively low incidence. Seed both provides the dissemination between crops and regions and is the immediate source of inoculum in the systemically infected plants. The airborne phase is local and transient and provides the limited external link between generations. Spores pass from infected heads to nearby healthy flowers, where infection occurs.

8C–2.5 Control

8C–2.5.1 Quarantine

The U.S. Department of Agriculture currently maintains a wheat quarantine, administered by the Animal and Plant Health Inspection Service, aimed at preventing the bringing in of Karnal bunt and foreign strains of flag smut. The People's Republic of China has a similar quarantine against dwarf bunt. Quarantines may be useful because these are diseases of limited geographic distribution, interregional or interconti-

nental spread appears possible only by infested grain or plant parts, and they may become endemic once established in the soil.

8C-2.5.2 Seed Treatment

Both chemical and physical means have been used in seed treatments to protect wheat from smut diseases.

8C-2.5.2.1 Chemical Treatment. Because of the nature of infection by wheat smuts, seed treatment has thus far been the only economically effective way of using chemical fungicides. Treatment of seed has been viewed as a means to protect against the smuts since the earliest approaches to these problems more than two centuries ago (Tillet, 1755). Chemicals are highly useful in some aspect of control of each of the wheat smuts. They have been most effective for common bunt, which is now almost completely controlled in developed countries largely through seed treatment, supplemented by host plant resistance (Hoffmann, 1982). Chemicals used have progressed from HCHO through Cu compounds and forms of organic Hg to polychlorobenzenes and systemic organic fungicides. Where seedborne inoculum is the only source of the problem, control came early. In regions of drier soils, such as the Pacific Northwest of the USA, soilborne inoculum posed a less readily treatable problem (Hoffmann, 1982). Use of the polychlorobenzenes, which were first studied in France, solved this more difficult problem in the Pacific Northwest, beginning in the mid-1950s (Holton and Purdy, 1954; Holton, 1967). Subsequently, a large number of more recently developed chemical formulations also effectively control both seed- and soilborne common bunt when used as seed treatments (Hoffmann and Waldher, 1982).

Dwarf bunt, being essentially soilborne and with a much later time of infection in the development of the wheat plant, is even more difficult to control than the soilborne phase of common bunt (Hoffmann, 1982). The polychlorobenzenes were found to be effective as soil drenches (Purdy, 1957), but such practices, although used in Europe, have not been considered feasible in the USA. Thiabendazole, or 2-(′-thiazolyl)-benziniadazole, a systemic fungicide, has some efficacy as a seed treatment for the control of dwarf bunt when seeding is delayed (Hoffmann, 1971). Although registered as a seed treatment in some states, its use has not been great, and chemicals are not currently a significant part of dwarf bunt control (Hoffmann, 1982).

Flag smut also can be both seed- and soilborne and provides problems for chemical control of the soilborne phase similar to those of dwarf bunt. Several of the newer systemic fungicides were found to be useful (Metcalfe and Brown, 1969; Line, 1972). However, complete control of the soilborne phase on highly susceptible cultivars is difficult to attain by seed treatment alone. The most effective control appears to be a combination of moderate resistance and seed treatment.

Fungicidal treatment also has been studied for the control of Karnal

bunt (Joshi et al., 1983), but the nature of the disease cycle and epidemiological pattern, with soilborne teliospores and floral infection, greatly limit the potential of seed treatment. Its main function may be to limit long-distance spread by infested seed.

Loose smut was not amenable to chemical seed treatment control prior to the development of systemic fungicides in the late 1960s, because of the protected internal location of the pathogen within infected seeds. The development of systemic fungicides (von Schmeling and Kulka, 1968) which can be used as seed treatments but persist in the seedling plants and eliminate the loose smut fungus from previously infected plants has revolutionized the control of loose smut of wheat (Jones and Collins, 1971; Wiese, 1977). With suitable effort this disease should now be completely controllable.

8C-2.5.2.2 Physical Control. Appropriate applications of heat were found very early to eliminate loose smut infection from infected seed without greatly harming the seed. A standard hot water treatment was developed by Jensen (1888) in Denmark, and solar methods (Bedi, 1957) have been used by small farmers in India (Holton, 1967). Although widely promoted in earlier extension programs, hot water treatment is currently impractical for individual farm use. A large-scale mechanized system for hot-water treating large seed lots was developed by the Indiana foundation seed agency (Agricultural Alumni Seed Improvement Assn., Inc.). Prior to the advent of systemic fungicides this was effectively used for custom treating and for the treatment of foundation seed stock to prevent widespread distribution of loose smut and particularly of specialized races in seed of new cultivars.

8C-2.5.3 Disease-Free Seed

Because loose smut is totally seed transmitted between crops, any means that will ensure that the seed is free from infection will control this disease. The modern systemic chemicals can accomplish this, but disease-free seed will achieve the same purpose. Microscopic methods were initially developed by Simmonds (1946) to detect loose smut infection in seed lots. This allows for a choice between seed lots or for determining the need for seed treatment of the lot to be planted (Russell and Popp, 1951). Statewide programs have been established to provide this service for the similar disease in barley (Morton et al., 1960).

8C-2.5.4 Host-Plant Resistance

Genetic resistance has been an important part of control for all the wheat smuts. Specific genes for resistance to common bunt, dwarf bunt, and loose smut are tabulated by McIntosh (1983). The occurrence of races of the smut fungi with specific virulence that can overcome the specific resistance of the host greatly increases the difficulty of attaining long-term, durable, effective control (Holton, 1967). Because the smut

fungi go through a sexual stage each infection generation, recombination of virulence genes and reselection for a broader combination of genes that may overcome existing resistance can readily occur.

Major breeding efforts have been made to develop multiple-gene resistance against common and dwarf bunts. It has been shown that the same genes conferring resistance to common bunt also function against dwarf bunt (Trione, 1982). In the absence of supporting seed treatment, these have not been as effective as for common bunt, where the integration of control measures is successful. Very limited effort has yet been made to identify and exploit a nonspecific type of resistance to the bunts (Hoffmann, 1982).

For flag smut, it is essential to use resistant cultivars, as seed treatment alone is not fully effective (Purdy, 1965). This again provides a form of integrated control that is more useful than either measure alone.

Resistance to Karnal bunt has not been identified, but the disease has been observed to increase with a change in predominant cultivars in India (Joshi et al., 1983). It is believed that some of the older Indian cultivars possessed a degree of resistance that was later lost in the absence of an active program in breeding for resistance. Systematic efforts to locate and transfer resistance have been initiated (Gill et al., 1983).

Excellent resistance to loose smut has been identified (Fischer and Holton, 1957; Gaskin and Schafer, 1962; Larose and Vanderwalle, 1937), and has been effectively incorporated into widely grown cultivars (Schafer et al., 1968). Histological studies showed that resistance can occur at several points in the infection cycle, including ovary resistance, embryo exclusion, inhibition of penetration of the growing point, reduction of growing point infection during plant development, differential internode elongation, and seedling or embryo death that eliminates the infected plants (Gaskin and Schafer, 1962).

8C-2.5.5 Cultural Practices

Variation in planting date may vary the amount of either common or dwarf bunt in the subsequent crop. Plants with many tillers or which have not yet emerged at the time of dwarf bunt infection have a lower incidence of dwarf bunt than those between these extremes. Thus, either early or late planting may reduce incidence of this disease (Hoffmann, 1982). Shallow planting favors dwarf bunt; deep planting favors common bunt.

Rotation with nonhosts has been found to reduce both flag smut (Purdy, 1965) and Karnal bunt (Joshi et al., 1983). Time of heading, which may be influenced by planting date, has been related to incidence of Karnal bunt (Gill et al., 1983). Irrigation schedules appear to be important in respect to Karnal bunt.

8C–3 WHEAT POWDERY MILDEW

Like the rust diseases, powdery mildews comprise a widely spread, uniquely appearing group of fungal diseases that attack many host plant species. Also, as with the rusts, the causal fungi are obligately parasitic and do not colonize nonliving plant tissue.

8C–3.1 Disease

8C–3.1.1 Description

Powdery mildew of wheat is well named, being recognized by the powdery, external growth of the mycelia and conidia (the vegetative strands and spores) of the causal fungus on leaf surfaces. When extremely severe this has the appearance of a white fur coat on the plant surfaces. In later stages this is embedded with superficial, dark, round, fungal fruiting structures known as cleistothecia, which develop in the surface powdery growth (Bruehl, 1967) (Fig. 8C–13).

8C–3.1.2 Early History

Powdery mildew does not appear to have been important on cereals until late in the 19th century (Hermansen, 1968), likely because of the low level of fertilization in early production practices. Specialization in parasitism between host species into formae speciales of *Erysiphe graminis* was demonstrated by Marchal in 1902; specialization in parasitism between wheat cultivars, into races of forma specialis *tritici*, was demonstrated by Mains in 1933 (Hermansen, 1968).

8C–3.1.3 Crop Production Limitation

Powdery mildew can occur wherever wheat is grown but is severe only in the cooler, moist, temperate regions, or during such season of the year. It is considered a damaging disease throughout much of Europe, in the southwestern USSR, and in the eastern- (Broscious et al., 1985) and westernmost parts of North America, including much of the southeastern USA (Jenkyn and Bainbridge, 1978). Kingsland (1982) considered powdery mildew the most important disease of wheat in South Carolina, but damaging only in those years when initiating in February or early March. With such early infection, yields were reduced 25 to 35%. Experimental data from Indiana showed 16% loss (Shaner, 1972). In Europe, yield losses in experiments can exceed 20%. Estimated losses from annual surveys in England and Wales range from 2 to 5% (Jenkyn and Bainbridge, 1978). The last overall U.S. loss figure was given as 0.4% (LeClerg et al, 1965).

Fig. 8C–13. Powdery mildew of wheat. (Photo by Illinois Agric. Exp. Stn., from M.V. Wiese 1977, *Compendium of Wheat Diseases.* Reprinted by permission of the American Phytopathological Society, St. Paul.)

8C–3.2 Pathogen

8C–3.2.1 Taxonomy

The powdery mildew fungi comprise the fungus family Erysiphaceae. All species are obligate parasites on plants. Yarwood (1978) defined this group as "those fungi with white superficial hyphae on aerial parts of living plants, with large one-celled conidia produced terminally on isolated aerial unbranched conidiophores and with haustoria in the epidermal cells of their hosts." He included seven genera in the family. These parasitize over 7000 host species of angiosperms, all dicotyledons except for the grasses (Yarwood, 1973).

Erysiphe graminis DC. ex Merat is the only species attacking grass

hosts and includes many specialized forms on different grass species, with that on wheat being forma specialis *tritici* E. Marchal (Bruehl, 1967; Wiese, 1977). Strains on different grass genera do not normally cross-infect (Jenkyn and Bainbridge, 1978). *Erysiphe graminis* is characterized by large digitate haustoria (Yarwood, 1973) (Fig. 8C–14).

8C-3.2.2 Life Cycle

The powdery mildew fungi are obligate parasites of their living host plants. Like the cereal rusts they cause only localized infections. They possess both an asexual and a sexual spore stage, both on the same plant. Young infections on the plant surfaces produce chains of conidia, the asexual spore stage, on short conidiophores extending from the vegetative hyphae. Later a sexual process leads to the dark, thickwalled cleistothecia, which contain ascospores, the sexually derived spore stage. Either conidia or ascospores may infect the leaf surface, leading to new infections.

8C-3.2.3 Cytology

The parasitic stage of *E. graminis* is haploid (Yarwood, 1978), in contrast to the dikaryotic condition in the rust and smut fungi. This allows for immediate expression of mutations for virulence. The fungus is heterothallic (Bruehl, 1967), thus needing two strains to form the sexual stage. Cells of the inner walls of the cleistothecia are dikaryotic; there is a short diploid phase followed by meiosis to form the haploid ascospores contained in delicate saclike asci within the thick-walled, durable cleistothecia (Yarwood, 1957).

Fig. 8C–14. Haustorium of *Erysiphe graminis* in wheat epidermal cell. (Photo by the Department of Plant Pathology, Washington State University, from M.V. Wiese 1977, *Compendium of Wheat Diseases.* Reprinted by permission of the American Phytopathological Society, St. Paul.)

8C–3.3 Pathogenesis

8C–3.3.1 Histology

Infection of wheat by *E. graminis* occurs only in epidermal cells. A short primary germ tube does not penetrate, but apparently establishes a water relationship with the host cell which is needed under arid conditions for subsequent penetration [as shown by Carver and Bushnell (1983) for barley mildew *E. graminis* DC. f. sp. *hordei* Em. Marchal]. A second germ tube is produced and quickly forms an appressorium, from which an infection peg develops. Penetration is directly through the cuticle and cell wall. Even prior to the formation of the peg, host cytoplasm aggregates beneath the appressorium to form a papilla on the inner surface of the cell wall (Jenkyn and Bainbridge, 1978). When infection is successful, penetration occurs through the papilla, and the infection peg invaginates the host plasmalemma and enlarges into a typical digitate haustorium. The haustoria establish a nutritive relation with the host cells (Bushnell and Gay, 1978) and are the only part of the pathogen which is inside the host plant (Bruehl, 1967). As the fingerlike lobes of the haustorium develop, a surface hypha grows from the appressorium. This hypha elongates and branches, and additional hyphae grow, leading to the development of the superficial fungal colony. Secondary haustoria are then produced from this colony, and both the internal (haustoria) and external (surface hyphae) portions of the colony continue to grow. Conidiophores and conidia develop about 4 days after infection. A colony eventually may have more than 1000 haustoria and conidiophores, with as many as 80 of the elaborately branched haustoria in a single host epidermal cell. There is typically one haustorium for about three hyphal cells (Jenkyn and Bainbridge, 1978).

8C–3.3.2 Physiology

The effect of powdery mildew infection on the immediate host tissue is much like that of rust infection, in that both groups are biotrophs. It was early determined that carbohydrates are needed in the host tissue to support infection (Trelease and Trelease, 1929; Scott, 1972). Subsequently, it was found in pioneering studies of Allen and associates that respiration increased in mildew-infected wheat tissue (Bushnell and Allen, 1962; Scott, 1972). Green islands are produced as induced healthy areas around the immediate infection sites to which nutrients are mobilized and in which carbohydrates are deposited (Bushnell, 1967; Bushnell and Gay, 1978). These phenomena imply that energy is needed for the parasite's development and regulation is provided to enhance this to the detriment of other portions of the mildew-infected plant.

8C–3.4 Epidemiology

Production of conidia is continuous in chains on the conidiophores, and is optimal at about 20° C and 100% relative humidity. Conidia are

passively released as a result of wind and rain and collect mostly on surfaces within the leaf canopy (Jenkyn and Bainbridge, 1978). Spore germination, leading to infection, is optimum at high humidity, but in the absence of free moisture (Yarwood, 1957; Bruehl, 1967). Powdery mildew fungi are among the very few fungi that do not require free moisture for germination. Successive cycles of infection may occur on plant surfaces during the crop season from the asexually produced conidia. As the infections age, they develop the dark, enclosed cleistothecia in the mycelial mat, usually after conidial production has stopped (Jenkyn and Bainbridge, 1978). The cleistothecia contain the sexually produced ascospores, which are actively discharged and, like the conidia, cause reinfection on wheat. The cleistothecia may survive over winter on fall-sown wheat, with ascospore discharge providing the primary spring infection. Powdery mildew also may overwinter as early stage vegetative fall infections on surviving leaves of winter wheat. Although the spores appear delicate, they may be carried long distances by air, to infect crops in other areas, as shown for barley by Hermansen and Wiberg (1972).

8C–3.5 Control

8C–3.5.1 Host-Plant Resistance

Use of resistant cultivars is the principal means of control. Much of the resistance is highly specific, and the major disadvantage has been the short duration of effectiveness. This has resulted from the occurrence of specific virulence in the mildew pathogen which inhibits the effect of the host resistance (McIntosh, 1978). A series of host resistance genes has been described, with several alleles at some loci (McIntosh, 1983). Near-isogenic lines possessing these genes have been developed (Briggle, 1969). Virulence to wheat cultivars possessing such genes singly has been reported in the pathogen for all such resistance genes that have been used extensively. However, both pyramiding of resistance genes and use of multilines have been proposed to provide more durability of resistance (McIntosh, 1978). Genetic studies of host resistance and pathogen virulence were reviewed by Ellingboe (1978).

Resistance characters that appear more general in nature and that are more durable in effect also have been reported (Roberts and Caldwell, 1970; Shaner and Finney, 1977). Excessive susceptibility is often associated with greater succulence of tissue, and many wheat cultivars become less susceptible to powdery mildew as the plants mature. There is a range of varying degrees of response of wheat cultivars to mildew infection. Some of these intermediate responses appear to have been long lasting (Shaner and Finney, 1977).

8C–3.5.2 Cultural Factors

8C–3.5.2.1 Nitrogen Usage. Various nutrients have been shown to influence the suceptibility of wheat to mildew, although the effects re-

ported have sometimes been contradictory. This may be due to interactions. Nitrogen has the most consistent effect, and typically increases the severity of mildew (Broscious et al., 1985). Other nutrient elements, in contrast, usually increase resistance, but only in plants initially deficient in such elements. The only important recommendation in fertilizer usage, beyond that for optimum crop growth and yield, is to avoid excessive N (Shaner and Finney, 1977; Jenkyn and Bainbridge, 1978).

8C-3.5.2.2 Sanitation. Because mildew can build up to epidemics so quickly from small inoculum sources, any factors that reduce initial inoculum have limited practical use. However, sanitary practices may at times be useful. Burying or destroying crop residue prior to ascospore discharge from the cleistothecia or prior to planting of the next crop may limit the initial inoculum available for fall-sown wheat (Jenkyn and Bainbridge, 1978).

8C-3.5.2.3 Separation of Crops. Spring and winter wheats are seldom grown in quantity in the same areas in mildew-favorable environments. However, the avoidance of a large source of inoculum, such as a winter crop in a spring crop region, is desirable. In this context, winter barley has been legislatively prohibited in Denmark, so as to reduce the level of inoculum available for the more important spring barley crop (Jenkyn and Bainbridge, 1978).

8C-3.5.2.4 Other Factors. Studies on the effects of row spacing, seeding depth, seeding rates, and their interactions with N fertilization have been conducted. These either did not show differential effects or have not been consistent between studies (Broscious et al., 1985).

8C-3.5.3 Chemical Control

Fungicides are used intensively for control of powdery mildew on various higher unit value fruit and vegetable crops. Because of the lower unit value of the cereal crops in relation to the costs of control, fungicides have been less useful on cereals. However, with recent more intensive crop production, this is changing in some regions. Use of fungicides on cereals to control mildew and other foliar diseases is now most common in Western Europe (Jenkyn and Bainbridge, 1978). Sulfur, in various forms, is the historic fungicide used. Numerous organic fungicides have been developed in recent years (Bent, 1978). Among these triadimefon has been used commercially on wheat in the USA (Kingsland, 1982), and other fungicides are in an experimental stage.

8D Virus Diseases of Wheat

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The recognition that viruses cause diseases in wheat is relatively recent, dating from the early 1920s. With each passing decade, the number of known viruses infecting wheat increases and estimates of losses resulting from them increases. One complex of viruses, barley yellow dwarf (BYDV), is now considered as possibly the most serious disease of small grains worldwide (Briggle, 1984). Three other widespread viruses are soilborne wheat mosaic virus (SBWMV), wheat yellow mosaic virus (WYMV) and its North American strain, wheat spindle streak mosaic virus (WSSMV), and wheat streak mosaic virus (WSMV). The emphasis in this section will be on the above four viruses and on general properties of viruses and virus diseases of wheat. Other viruses will be discussed only briefly; more information on them may be found in: Jackson et al., 1981; McKinney, 1967; Slykhuis, 1967, 1976; Wiese, 1977.

8D–1 NATURE OF VIRUSES

Viruses are infectious agents containing only the essentials for survival, a genome and its protective protein coat. Plant viruses may have either an RNA or a DNA genome. The genome is small, with a molecular weight of 2 to 5 million, about one-millionth the size of the wheat genome. Virus RNA genomes mutate as much as a millionfold faster (on a per replication-per-base basis) than DNA genomes (Holland et al., 1982). A plant virus culture is a collection of related mutants, the dominant mutant being the one that grows most rapidly under the particular conditions. Change of conditions, e.g., of host plant or temperature, may lead to predominance of a different mutant. Some of the frequent mutations are those that control disease symptoms, vector transmissibility, and genome size. This variability has implications for breeding for resistance. Breeding for resistance to RNA viruses should not necessarily follow the pattern

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of breeding for resistance to pathogenic fungi, where attention must be paid to virulence genes of the pathogen. With RNA viruses, it may be sufficient to breed for resistance to a mixture of current field strains, unless there is evidence that the virus has stable virulence genes that respond differently to specific host resistance genes.

The infectious viral particle, also called a *virion*, is analogous to a fungal spore in that it is a stable, nonmultiplying stage by which the virus is transferred from one plant to another. Inside the cell, nucleic acid and protein of the virion separate before replication. The steps in the replication are not fully understood, but they depend in part on host enzymes and organelles. A limited number (perhaps up to 10) of proteins and RNAs besides those of the virion are specified by the viral nucleic acid. The function of a few of these accessory proteins and RNAs are known. The functions of most are unknown, as are the molecular mechanisms by which viruses damage hosts.

Mosaic viruses interfere with chloroplast development when they infect immature cells of very young leaves during systemic invasion of the plant. The virus usually does not multiply equally in all cells, nor is chloroplast damage uniform; this yields a *mosaic*, i.e., a pattern of light-green or yellow areas mixed with dark green areas. If all cells are invaded, the leaf may be almost uniformly yellow or light green.

The phloem-limited viruses, such as BYDV, interfere with translocation (Jensen, 1969, 1973). Carbohydrates accumulate in the leaves and glumes predisposing them to invasion by fungi (Jensen, 1969b). At the same time, the leaves show a variety of discolorations (yellowing or reddening depending on the species responses) that are reminiscent of senescence or nutrient deficiencies.

Viruses stunt shoots and roots and may cause growth changes resembling hormonal imbalances. Tiller number may be reduced, head size reduced, and kernels shrunken. Yield is reduced, and the resultant shrunken kernels planted as seed may germinate poorly to produce seedlings of low vigor.

There are several steps in the invasion of a plant by a virus and development of symptoms. Infection begins when a vector, usually an insect, mite, or fungus, introduces the virus into a cell. The virus multiplies in the initially infected cell, invades and multiplies in adjacent cells, and moves into and through the phloem to invade the plant systemically, including meristematic tissue. Once meristematic tissue is invaded, usually (but not always) all subsequently formed tissues are infected. Partial infection of meristematic cells may lead to a streaking symptom in monocotyledons.

All of these steps are influenced by plant genotype as well as by growing conditions, particularly temperature. Low temperature delays virus movement more than it inhibits virus replication. Resistance of a wheat cultivar, in the sense of not suffering yield loss, may be caused by several factors. The vector may not like to feed on the plant. The plant

may be difficult to inoculate, i.e., there may be a low probabiliity of virus replication in the initially infected cell. Virus movement may be slow. Only part of the meristematic tissues may be infected and therefore systemic invasion of new leaves and roots may be incomplete. Finally, even though a cell is infected, its functioning may be less disrupted than that of another cultivar. With such a multitude of events entering into resistance, it is no wonder that breeding for resistance is often complex.

8D–2 EPIDEMIOLOGY OF VIRUSES WITH AERIAL VECTORS

Most viruses of wheat are spread by aphids, leafhoppers, planthoppers, beetles, mites, or the root-inhabiting fungus *Polymyxa graminis* L. One, barley stripe mosaic virus, is pollen- and seed-transmitted. With that exception, the viruses must be transmitted anew to plants in each crop of wheat. Knowledge of how viruses spread is essential to understanding why epidemics occur, and often also to the formulation of control recommendations.

High insect populations occur episodically. Likewise, insects migrate periodically. The timing of high insect populations and migrations in relation to stage of crop development, the percentage of insects that are viruliferous, and their efficiency in transmitting the virus all are factors that determine whether an epidemic of insect-transmitted virus disease will occur. The net result is that incidence of disease varies from year to year, with epidemics being the exception, though high levels of infection may occur in individual fields most years.

Changing agricultural practices can change the incidence and severity of WSMV, BYDV, and other wheat viruses with aerial vectors. Increased acreages of irrigated maize (*Zea mays* L.) or of spring grains in traditional winter wheat areas provide potential sources of vectors and virus to infect fall-sown wheat. In Great Britain and northern Europe a switch during the last several years from spring to winter cultivars and increasingly early sowing of these in the autumn has increased the incidence of BYDV (R.T. Plumb, Rothamsted Experiment Station, UK, personal communication, 1983). The BYDV in New Zealand caused losses of about 25% every year in the early 1960s, but not a decade later after cessation of use of DDT for insect control (Smith, 1963b; Burnett and Smith, 1976). The DDT may have killed more predators than aphids. Increased use of minimum tillage or no-tillage may provide more summertime volunteer wheat than conventional tillage if the herbicides used are ineffective against wheat. Some newer, long-lasting but highly specific herbicides are very effective in killing all weeds, but they do not identify volunteer wheat as a weed. Double-cropping with soybean [*Glycine max* (L.) Merr.] or other crops planted after harvest offers potential for volunteer wheat to support virus and vector over the summer. Introduction of perennial wheat, if

such were developed, would be potential disaster from the viewpoint of virus diseases.

8D–2.1 Barley Yellow Dwarf Virus

The most widespread virus of wheat, BYDV, is transmitted by at least 23 species of aphids (for a list with current names and synonyms see Jedlinski, 1981, and A'Brook, 1981b). One vector, the greenbug, overwinters in the southern USA or Mexico and is blown north on strong, southern jet winds in the spring (Wallin et al., 1967). A severe epidemic of BYDV in 1959 was attributed to an early and heavy infestation of greenbug (Bruehl, 1961). Other cereal aphids may overwinter on grasses (e.g., *Sitobion avenae* F.) or as an alternate life-cycle form on trees or shrubs (e.g., *Rhopalosiphum padi* L.). These aphids move into grains in the spring and reach peak populations in late spring or summer, the time depending on the aphid species, latitude, and weather (Plumb, 1983). The migrating aphids probably acquire BYDV from infected grasses, perennials, winter annuals, or cereals that live over the winter. Primary infection in a field results from feeding of migratory aphids that acquired the virus from a reservoir host. Secondary infection results from aphids that acquire virus from an infected wheat plant and carry it to adjacent plants. With BYDV, a cluster of infected plants typically results when disease incidence is low (Gill, 1980).

There are numerous grass hosts that provide potential reservoirs of BYDV. Rochow (1961) listed 84 susceptible species of Gramineae. Incidence of virus-infected grasses may be high. More than 50% of the plants in ryegrass (*Lolium perenne* L.) pastures in some areas of New Zealand were infected with BYDV transmissible by *R. padi* (with a high of 84% infection) (Latch, 1977). Grafton et al. (1982) reported that 60% of 136 tall fescue (*Festuca* spp.) plants collected from 90 counties in Missouri had BYDV. The plants were symptomless and virus was detected by transmission tests. Fargette et al. (1982) found about 50% of grass plants in Indiana infected with BYDV. Similar high values have been reported in Scotland (70%) (Holmes, 1977), Northern Ireland (70 and 86%) (Cooper, 1977), and England and Wales (93% of fields of ryegrass infected) (Doodson, 1967). However, the amount of BYDV transmitted from grasses to adjacent cereals is uncertain, because the predominant strains in the cereal crops do not always match those of the grasses (Fargette, et al., 1982).

The spring and early summer aphids are important in incidence of BYDV in spring wheat and other cereals. For winter wheat, the important aphids are those that migrate and multiply in the fall and the important virus reservoir hosts are grasses or susceptible crops that are still alive and green when winter wheat sprouts (Plumb, 1983). In Montana, Yount and Carroll (1983) reported that epidemics of BYDV were correlated with high populations of *R. maidis* F. in September. The disease could be controlled by planting wheat after 10 September. In Washington, irrigated maize is an oversummering host. Brown et al. (1984) reported

that 61% of aphids, primarily *R. padi*, and 63% of the maize samples collected had BYDV. The naturally infected maize plants were symptomless, so the samples were not collected on the basis of symptoms. The BYDV-infected maize also has been found in France (Signoret and Alliot, 1981) and has been implicated as a source of aphids (mainly *R. padi*) and BYDV for infection of winter wheat (Dedryver and Robert, 1981). In Wales and southern England, a flight of aphids in September and October can result in infection of winter cereals with BYDV (A'Brook, 1974). Late seeding of winter grains reduces incidence of BYDV except in areas where aphids are active through the winter.

Presence of several strains transmitted by different aphid species complicates the epidemiology of BYDV. They vary in pathogenicity and in host range of reservoir plants. Biotypes of one vector, the greenbug, vary in transmission efficiency (Rochow, 1960). The most prevalent aphid is not always the most important vector, partly because of feeding preference. A favorite host plant of the greenbug is sorghum [*Sorghum bicolor* (L.) Moench], which is a poor host of BYDV, but *R. padi* favors maize, many cultivars of which are good hosts of BYDV. The epidemiology of BYDV is complex and needs much additional study before it is fully understood.

8D–2.2 Wheat Streak Mosaic Virus

Another serious disease of wheat with an aerial vector is WSMV, spread by an eriophyid mite, *Eriophyes tulipae* Keifer in North America and France (Slykhuis, 1953; Poinso et al., 1981) and in Yugoslavia by *E. tosichella* Keifer (Tosic, 1973). The mite is invisible to the naked eye, being only 250 μ long. It is wingless and depends on the wind for dispersal. The mites are usually found on unexposed young leaves in whorls or inside rolled leaves. As plants mature, mites migrate to the heads, the last succulent part of the plant. At certain times, the mites leave protected parts of the plants to crawl to leaf tips or other exposed areas where they become airborne in the wind. Mites must be nymphs when they acquire the virus if they are to transmit it (Orlob, 1966). Once they are viruliferous, mites can transmit the virus for several days (Slykhuis, 1955).

Both mite and virus have several hosts among wild grasses, but relatively few in common (Slykhuis, 1955; Connin, 1956; Sill and Aguisiobo, 1955; Staples and Allington, 1956; Tosic, 1973). However, the mites do not seem to build up to as high a population on these plants as on wheat. Wheat streak mosaic virus has caused more loss to winter wheat than to spring wheat (McKinney, 1967). Spring wheat is susceptible, and epidemics have occurred in areas where both spring and winter wheat are planted. If weather conditions are such that the spring and winter wheat crops overlap, serious WSMV epidemics may occur in either or both (Lamey and Timian, 1979; Atkinson and Slykhuis, 1963).

The key point in the epidemiology of WSMV on winter wheat is the presence of oversummering hosts on which viruliferous mites build up

to large numbers. Wild grasses, such as can be found almost any year in any winter wheat field in the Great Plains of North America, probably are a source of sufficient viruliferous mites to infect a small percentage of wheat plants. In some years in some locations, the grasses may supply sufficient viruliferous mites to heavily infect adjacent wheat fields. Annual *Bromus* spp. are thought to be such a source in South Dakota (S.G. Jensen, University of Nebraska, personal communication, 1983).

In the northern Great Plains of North America, the important summer host may be a late-maturing spring wheat crop or volunteer winter wheat that starts growing before harvest, often as a result of hail storms (Staples and Allington, 1956). Early germination results in infestation of the volunteer plants with mites and infection with virus. Severe epidemics occur in the following crop downwind from fields of diseased volunteer wheat, with the incidence of virus decreasing from 100% to a few percent over a distance of 2 to 8 km. Yield loss can vary from nearly 100% to undetectable, depending on cultivar, strain of virus, and weather. Destroying the volunteer wheat at least a week before planting the new crop controls the disease in these situations. The mites can survive for several days in leaves severed from plants and covered with soil (Slykhuis, 1955).

In Kansas and Oklahoma, epidemics sometimes cannot be traced to volunteer wheat in adjacent fields of the previous summer. In these areas of the southern Great Plains, wheat is often planted relatively early (September), to provide forage. In warm autumns there is ample time for extensive secondary spread of virus and mites within the field, resulting in a high incidence of infection even though primary infection is low. Some winters the weather is mild enough for mites to be active and wheat to grow throughout the winter. Infection of winter wheat in early spring leads to substantial losses.

Other potential oversummering hosts of mites and WSMV are foxtail millet (*Setaria* spp.) and irrigated maize (Staples and Allington, 1956; How, 1963). Both have been circumstantially implicated as sources of inoculum for wheat in a few fields in western Nebraska, and maize for a considerable acreage in western Oklahoma.

WSMV is a serious disease of winter wheat in the western part of the Great Plains of North America, where fields are planted to wheat every other year and fallowed in intervening years. The virus has been reported in California, Washington, Idaho, Indiana, Ohio, Illinois, and Iowa (McKinney, 1967; Gordon et al., 1981) and probably occurs throughout the soft winter wheat area of USA. However, with some exceptions (Palm, 1982), WSMV has not been an important disease of winter wheat in areas with annual cropping. The reason probably lies in factors influencing the population dynamics of the mite.

8D-3 EPIDEMIOLOGY OF SOILBORNE VIRUSES

The epidemiology of soilborne viruses is different from that of viruses with aerial vectors. *Polymyxa graminis* L., an obligate fungal pathogen

of wheat roots, is the vector of both SBWMV and of WYMV (WSSMV) (Estes and Brakke, 1966; Slykhuis and Barr, 1978). *Polymyxa graminis* infects plants by biflagellate zoospores released from intracellular sporangia or germinating resting spores (Ledingham, 1939; Rao, 1968; Barr, 1981). The fungus survives the summer in resting spores. By itself, the fungus causes no obvious damage in wheat or other hosts, but no controlled experiments to detect damage have been reported. *Polymyxa graminis*, or a fungus or fungi morphologically indistinguishable, infects wheat, barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), *Agropyron repens* (L.) Beauv., *Bromus inermis* Leyss., *B. tectorum* L., *Hordeum jubatum* L., sorghum, and maize (Barr, 1981; Langenberg, University of Nebraska, personal communication, 1983). *Polymyxa graminis* apparently carries SBWMV internally, because the zoospores cannot acquire virus in vitro, nor can virus carried by zoospores and resting spores be inactivated by acid, alkali, or antiserum to virus (Rao and Brakke, 1969; Brakke et al., 1965).

The SBWMV has not been reported in spring wheat. If spring wheat were to become infected, the virus probably would remain in the roots and the infection would be unnoticed (Brakke et al., 1965; Rao and Brakke, 1970). When wheat is planted in infested soil, the incidence of virus infection depends on susceptibility of the wheat cultivar, moisture and soil temperature, and date of planting. Less infection is obtained with late planting, which may be because of lower soil temperature.

Once soil is infested with the fungus and virus, it remains infested unless fumigated, a procedure too expensive to be a control method for wheat (McKinney, et al., 1957; Saito et al., 1964). However, the quantity of fungus and virus will depend on susceptibility of the plants that grow in the soil. Incidence of infection in a field will increase from year to year until essentially all plants become infected if susceptible cultivars are planted year after year. The incidence will decrease from year to year if resistant cultivars or nonsusceptible crops are planted. The extent of the area of infested soil increases from year to year, probably as a result of soil carried on tillage equipment, blown by the wind, or carried by water erosion. As of 1983, SBWMV has been found as far west as central Nebraska and (in irrigated fields) the Oklahoma panhandle. The disease occurs from there east through the rest of the USA, as well as in southern Europe and in Japan.

Wheat yellow mosaic virus (WYMV or WSSMV), also transmitted by *P. graminis*, occurs in Ontario, USA, India, France, and Japan (Brakke, et al., 1982; Slykhuis and Polak, 1969; Wiese, 1977; Usugi and Saito, 1979; Analwat et al., 1976; Signoret et al., 1977). Its epidemiology is similar to that of SBWMV, but the relative proportions of the viruses varies from place to place and their known ranges do not yet completely overlap.

8D–4 IDENTIFICATION

The most definitive diagnosis of virus diseases is by identification of the virion by serology, electron microscopy, size and properties of RNA or capsid protein, presence of inclusion bodies in host cells, transmission by a specific vector, or transmission to selective hosts. Serology is the most widely applicable, especially with the development of the ELISA test (Clark and Adams, 1977), which detects viruses present in low concentrations, even BYDV. Electron microscopy is quick and useful for preliminary identification of rod-shaped viruses. Serology combined with electron microscopy gives quick, very sensitive, positive identification of both rod-shaped and spherical viruses. Aphid transmission successfully identifies BYDV but is slow and labor intensive. Transmission to selective hosts and symptomatology have not been as useful for identification of wheat viruses as for those of some other crops. Both host range and symptoms are variable, depending on virus strain and growing conditions, so that the range of results with one virus overlaps that of another.

Field symptoms alone are not reliable for diagnosis of virus diseases of wheat. When viewing the growing crop from 3 m or more, one cannot distinguish virus symptoms from those due to root and crown rots, low fertility, herbicide residue, or other causes. If plants are infected with a mosaic virus, the youngest, partly expanded leaf of young plants will show a mosaic pattern. If this youngest leaf does not show mosaic, the plant probably is not infected with a mosaic virus. The mosaic on young leaves may not be present on older plants with SBWMV. Presence of mosaic on the youngest leaf is a reliable indication of a virus disease, but the type of mosaic pattern does not reliably distinguish one virus from another. Symptoms combined with pattern of occurrence in the field, cropping history, and cultivar response can give quite reliable diagnosis. Virus diseases usually do not infect 100% of the plants and some symptomless plants should be present among the diseased, whereas nutritional or herbicide residue problems usually affect every plant, though severity may vary from plant to plant. SBWMV usually occurs in localized areas of the field, especially along waterways, low, wet parts of the field, and old building sites. Intensity of WSMV infection is uniform, but may decrease downwind from the source of infection. Symptoms of SBWMV are yellowest early in the spring, when growth has just started; the infected areas will appear less yellow if inspected a few weeks later. Symptoms of WSMV, if anything, become more severe with time. BYDV does not give a mosaic on youngest leaves, but older leaves may be yellow, stiff, and more erect than usual. In North America, early fall infection of BYDV generally produces stunting, increased susceptibility to winter injury, and a reduction in numbers of tillers, heads, and kernels per head, whereas spring and early summer infection gives leaf discoloration (Cisar, et al., 1982b). In Great Britain and Europe, symptoms of BYDV on wheat usually include reddish, purplish, or yellow leaf coloration (R.T. Plumb,

Rothamsted Experiment Station, UK, personal communication, 1983). Infected areas often occur as circles of a few to several meters in diameter, scattered throughout the field. Other conditions and diseases produce yellowing similar to that of BYDV. Aster yellows produce symptoms on individual plants similar to those of BYDV (Gill et al., 1969).

Exceptions and variations to all of these generalizations are common. If the field situation is not typical or the identification is important, e.g., if it is the basis for whether to keep the field for harvest, it is best to confirm the field diagnosis by laboratory test. If the first laboratory test is at variance with field observations, additional tests on more samples are desirable. The presence of two or more viruses in a field is common. Frequently laboratory tests are done on only one or a few plants. There is a tendency to select for testing plants that show symptoms particularly clearly, but these may not be typical. The plant may have two viruses, or a virus infection in addition to a second disease, nutritional deficiency, or other problem.

Identification of viruses as the cause of a problem is especially difficult if the wheat has headed. The SBWMV is hard to recover or identify at this time, but the plants in infected areas are stunted, frequently with fewer tillers. Incidence of viruses with aerial vectors may be high because of late infections that cause little detectable damage. Allington and Staples (unpublished results) found that an average of 70% of the heads of nearly mature wheat collected from many fields over a few years in Nebraska had mites carrying WSMV, a figure much higher than the few percent of young plants that show mosaic in randomly inspected fields. A similar situation probably prevails with BYDV. A'Brook (1974) reports that 75% of the samples of wheat leaves collected from wheat in the milk stage in Wales and England in 1971 had BYDV. Each sample consisted of 10 leaves collected from a single field. Certainly, identification of virus in a few nearly mature plants from a field should be combined with other observations before the problems of the field are attributed to virus infection.

8D–5 LOSSES

With most virus diseases, the yield loss varies inversely with the age of plants at time of infection. For example, fall infection reduced grain yield by 63% and spring infection by 41% for 1723 selections of winter wheat (Cisar et al., 1982b). With spring grains also, the earlier the inoculation, the greater the yield loss (Gill, 1980).

When young plants of susceptible cultivars of wheat are inoculated with BYDV, the measured yield loss per plant is 40 to 90% (44%, Potter, 1982; 47–76%, Jensen et al., 1971; 64%, Gill, 1967; 63–87%, Gill, 1980; 27–58%, Carrigan et al., 1981; 62 and 81%, Fitzgerald and Stoner, 1967; 50–84%, Cisar et al., 1982a). Not only do BYDV and other viruses de-

crease yield but they also can result in shriveled grain of lower viability and quality (Gill, 1980).

Losses in individual fields at high infection rates may approach those cited for individual plants, but are less when averaged over a large area. Estimates for field losses for a country or state range from a high of 60% for Chile in 1979 (CIMMYT, no date), and 25% in New Zealand in the early 1960s (Smith, 1963b), to < 10% in the majority of estimates. Gill (1980) reported 7% loss in spring wheat in nine crop reporting districts of southern Manitoba in 1978. His is one of the most accurate estimates that have been made, since it was based on estimates of percentages of infected plants and experimental measure of yield of plants with different degrees of symptom development. It is difficult to estimate loss for any disease, but this is particularly so for BYDV, because it frequently does not produce visible symptoms in wheat except for stunting, which can have many causes. The incidence of BYDV and losses due to it may have been consistently underestimated.

In the 1920s, loss to SBWMV in fields of susceptible cultivars could be total (McKinney, 1937). In 1952, Koehler et al. (1952) listed losses of 0 to 80% for 53 cultivars of soft red winter wheat. Soft red winter wheats showing the rosette reaction had a yield loss of 80%, compared to 18% for those showing severe mosaic and 11% for those with mild mosaic (Bever and Pendleton, 1954). Kucharek and Walker (1974) reported 50% loss in infected areas of wheat fields in Florida. Losses up to 45% for hard red winter wheat in Nebraska (Palmer and Brakke, 1975) and up to 48% in Kansas (Campbell, et al., 1975) have been reported. Nykaza et al. (1979) compared resistant and susceptible isogenic lines and cultivars and found decreases in kernel weight, tiller number, test weight, plant height, and yield (range 3.3–45.2%, average 22% loss) due to SBWMV infection. Loss varied with site and season and appeared to be greater in years with prolonged spring temperatures below 17° C.

WSSMV has been reported to reduce yield up to 59% in individual plants and up to 40% in infected areas of a field (Slykhuis, 1970). A range of loss from 14 to 44% for susceptible cultivars was reported by Wiese et al. (1974).

WSMV causes up to 100% loss in severly infected fields. The loss decreases with decreased incidence and delayed infection to undetectable levels.

There are relatively few estimates of losses due to mosaic viruses as a percentage of the total crop. However, such estimates are regularly made in Kansas. The average estimated loss to SBWMV from 1976 to 1983 was 2.9% and to WSMV, 1.8%, with the maximum yearly loss being 7% to WSMV in 1981 and 5% to SBWMV in 1976 and 1977 (T. Sims and W.G. Willis, Kansas State Univerisity, personal communication, 1983). However, more severe losses have occurred in past years. An estimated loss of 5% of the crop to WSSMV in two counties of Ontario in 1967 to 1968 was reported by Gates (1969).

These estimates are sufficient to show that the virus diseases can be important if infection is widespread. In particular, any of these viruses can be serious for individual farmers, who may lose half or more of their crop.

Much anecdotal evidence exists indicating an increased susceptibility of virus-infected plants to winter-kill, root rots, and fungal foliar diseases. Thus, Cisar et al. (1982b) noted that wheat infected with BYDV in the fall of 1977 did not survive the following winter. However, it is difficult to obtain controlled experimental evidence. In an attempt to do so, Paliwal and Andrews (1979) and Andrews and Paliwal (1983) found only a slight decrease in winter hardiness. In regard to infection with two diseases, Potter (1982) found a 44% yield reduction for wheat infected with BYDV only, 33% with rust only, but 63% when infected with both rust and RYDV. An increased incidence of *Cladosporium* and *Alternaria* fungal species on heads of wheat infected with BYDV results in blackened heads and leaves, useful at times in determining incidence of BYDV, but also decreasing market value of grain because of discoloration (Ajayi and Dewar, 1983; Smith, 1963b). There is a possibility that BYDV may predispose plants to root rots (Smith, 1962). Potter (1980) found that BYDV alone reduced yield as much as BYDV plus mildew. BYDV-infected wheat is more susceptible to ergot (perhaps because of more open florets) than uninfected wheat, a relation which could lead to quality problems (H. Jedlinski, USDA, University of Illinois, personal communication, 1983). Adlakha and Raychaudhuri (1975) found an increase in *Helminthosporium sativum* lesions in wheat infected with WSMV.

A decreased susceptibility of virus-infected plants to other pathogens also may be observed. Varughese and Griffiths (1983) reported that barley infected with BYDV was less susceptible to leaf blotch and net blotch (*Rhynchosporium secalis* and *Pyrenophora teres*) than was barley not infected by virus.

8D–6 CONTROL

Incidence of all the cereal viruses in winter wheat can be decreased by planting late. In parts of North America, this means after the Hessian fly-free date, which varies from 16 September in central Michigan to 27 October in northern Georgia and from 20 September in northern Nebraska to 15 October in central Oklahoma (Gallun, 1965). Date of planting is also important for spring wheat, but in this case early planting should be beneficial so that the plants will be large before becoming infected and severe damage will be avoided.

Avoidance of crops that provide oversummering or overwintering hosts also should reduce incidence of virus diseases. Raising irrigated maize susceptible to BYDV or WSMV in certain traditional wheat-growing areas may be a source of virus diseases for the wheat, though the maize itself suffers little loss. Maize lines resistant to WSMV are available.

Approximately 60% of inbred lines in the NCR-2 Uniform Inbred Nursery over the past several years were resistant to WSMV (M.K. Brakke, unpublished data). Half of 10 maize cultivars were immune to BYDV (Panayotou, 1977). Overlapping crops of spring and winter wheats or other cereals could also provide continuous hosts for vectors and virus and a buildup of disease.

Weeds, grasses, and volunteer wheat may be a source of both WSMV and BYDV. Farmers adopting minimum till, no-till, and double-cropping practices should realize that volunteer wheat is a most dangerous weed from the viewpoint of controlling virus diseases. Control of volunteer wheat in the Great Plains of North America is essential to control of WSMV in hard red winter wheat. In Great Britain, aphids may survive the summer on volunteer wheat or barley to inoculate the autumn crop with BYDV. Likewise, grassy stubble or a previous grass crop of hay or pasture may provide viruliferous aphids (Plumb, 1983). Both aphids and mites will survive in a field after cultivation for a period of time depending on temperature, moisture, and thoroughness of cultivation. Survivors may be particularly effective in starting an epidemic, because they are in place to inoculate emerging plants promptly, leaving ample time for secondary spread.

As with other diseases, virus diseases of wheat can be controlled by breeding resistant cultivars. Good sources of resistance to SBWMV and WSSMV are available, and many commercial cultivars with resistance have been released. Resistant cultivars are not available for WSMV or BYDV, but available germplasm varies in tolerance (Qualset et al., 1973; 1977; Cisar et al., 1982a, 1982b; Rahman et al., 1974; Shaalan et al., 1966). The tolerance in some cultivars (e.g., Anza) and in wheat–*Agropyron* crosses is very good (Qualset et al., 1973; Cisar et al., 1982b). Tolerance is quantitatively inherited (Qualset et al., 1973; Cisar et al., 1982a; Tola and Kronstad, 1984). In a similar situation, resistant (tolerant) cultivars of oat (*Avena sativa* L.) were developed by a breeding scheme based on transgressive segregation (Jedlinski, 1972). It is still a question whether such a program will work for WSMV and BYDV resistance in wheat, although some optimism has been expressed in the case of BYDV (Cisar et al., 1982b). Resistance to WSMV is available in *Agrotricum*—wheat hybrids (Fellows and Schmidt, 1953; Larson and Atkinson, 1973; Wells et al., 1982), but is has proven difficult to transfer this resistance to commercially acceptable cultivars (Martin et al., 1984). This resistance appears to be based on hypersensitivity and its expression varies with the environment (Pfannenstiel and Niblett, 1978). Another approach is to breed cultivar resistant to the vectors (Martin et al., 1976). Pubescent wheats are less hospitable to mites and have fewer mites and less virus in the field (Harvey and Martin, 1980). Rye is resistant to the mite and this resistance has been transferred to the wheat–rye translocation cultivar Salmon (Harvey and Livers, 1975; Zeller, 1973). A mite-resistant line from a cross between cv. Salmon and cv. Sage averaged

58% less WSMV infection during 3 yr in Kansas than its virus- and mite-susceptible parent, Sage (Martin et al., 1984).

Timely spraying with aphicides prevents secondary spread and most yield loss due to BYDV (Plumb, 1983; Smith, 1963b). In the United Kingdom and New Zealand, proper planting dates and application of aphicides are recommended to control BYDV in autumn-sown cereals (A'Brook, 1981a; Plumb, 1983, 1984; Smith and Wright, 1984). Recommendations on when to spray in the United Kingdom are based on populations of migrating aphids and their ability to transmit virus (Plumb, 1983, 1984).

Soil fumigation can control soilborne viruses, but is generally not economical (Eversmeyer et al., 1983; McKinney, 1957; Saito et al., 1964). Crop rotation has not given satisfactory control of SBWMV (Koehler et al., 1952).

8D–7 CHARACTERISTICS OF THE VIRUSES

8D–7.1 Barley Yellow Dwarf Virus

The term *barley yellow dwarf virus* includes several related viruses (Rochow and Duffus, 1981). They all have roughly spherical virions 25 nm in diameter, a sedimentation coefficient of about 115 s, a capsid protein of Mr 24 000, a single-stranded RNA genome of Mr 2×10^6; they all are confined to the phloem, and are transmitted by aphids in a persistent manner (Rochow and Duffus, 1981; Rochow, 1970b). They differ in severity of symptoms, reactions with specific antisera, and transmissibility by different aphid species. BYDV can be transmitted by 23 species of aphids (Jedlinski, 1981; A'Brook, 1981b). Four of these can be used as differentials to separate BYDV into five strains, designated MAV, RPV, PAV, RMV, and SGV (Rochow, 1979). MAV is transmitted by *S. avenae*, RPV by *R. padi*, RMV by *R. maidis*, SGV by *Schizaphis graminum* R., and PAV by both *R. padi* and *S. avenae*. The different isolates may be transmitted infrequently by species of the differentials other than their usual vector. In addition, vector specificity may break down when aphids feed on plants infected with two isolates (Rochow, 1970a; Rochow and Gill, 1978). Depending on the age of the plants and timing and sequence of inoculation, both synergism and cross-protection have been observed in plants infected with multiple strains of BYDV (Smith, 1963a; Halstead and Gill, 1971; Jedlinski and Brown, 1965). Differential tolerance of host cultivars to BYDV strains has been observed, but generally cultivars tolerant to one strain are tolerant to others.

Barley yellow dwarf virus infects at least 84 species of monocotyledenous plants, including oat, wheat, barley, and maize (Rochow, 1961). BYDV does not infect dicotyledenous plants, but similar viruses do, and many of them are serologically related to BYDV (Rochow and Duffus, 1981). One of them, beet western yellows virus, infects oat and is ser-

ologically related to the RPV strain of BYDV. It is possible that some of these other viruses could mutate to give new strains of BYDV.

BYDV has been reported from North America, South America, Europe, Africa, New Zealand, Australia, and China. One of the major problems in studying BYDV is detection. Typical symptoms include yellowing of leaves starting at the leaf tip, an upright posture of leaves and heads, thickened and stiff leaves, stunting, and reduced tillering. However, typical symptoms are not always observed. Fall-infected winter wheat often shows no symptom other than stunting and low tillering (Cisar et al., 1982b). The virus occurs in low concentration. Often as little as 50 μg per kg of leaf can be isolated (Rochow and Brakke, 1964). Virus yields can be increased to 1 to 4 mg kg^{-1} by growing plants at cool temperatures (below 25° C), harvesting when virus concentration is a maximum, and using improved grinding procedures (Paliwal, 1978; D'Arcy et al., 1983). The highest concentrations of virus were found in roots (D'Arcy et al., 1983). Adding to the above problems of detection, BYDV is not sap transmissible. Many standard methods for virus identification do not work with BYDV. Until recently, reliable identification of BYDV depended on aphid transmission, a slow and labor-intensive procedure, complicated by the fact that no one aphid species transmits all isolates of BYDV. Recently, the serological ELISA test, (Clark and Adams, 1977) has been adopted to identify BYDV (Lister and Rochow, 1979; Rochow, 1982). The ELISA test provides a tool by which we can finally determine just how much of a problem BYDV is in wheat.

8D–7.2 Wheat Streak Mosaic Virus

Wheat streak mosaic virus is sap transmissible. Its virions are long flexuous rods, 700 × 13 nm, that occur in low concentrations, 10 to 100 μg per gram of leaf (Brakke, 1971a). It has a single-component, single-stranded RNA genome of Mr 2.8×10^6 and a capsid protein of apparent molecular weight by SDS gel electrophoresis varying from 40 000 d to 50 000 d as the gel concentration is changed from 12 to 5% polyacrylamide. A series of five smaller proteins with molecular weights down to 30 000 d, presumably degradation products of the capsid protein, are present in minor amounts in virions purified from young leaves. However, increased amounts of degraded capsid protein are found in virions purified from old leaves and in some preparations only the 30 000 d protein is present (M.K. Brakke and L. Lane, unpublished data). Pinwheel inclusions are found in cells infected by WSMV and extracts of these cells have a protein of Mr 66 000, present in amounts of about 100 μg per gram of leaf that is a component of the pinwheel inclusions (White and Brakke, 1983; Brakke et al., 1986.

WSMV isolates give symptoms ranging from a mild mosaic to severe chlorosis. Since all wheat cultivars are susceptible, maize cultivars have been proposed as differential hosts to separate strains (Niblett et al., 1976). However, Carroll et al. (1982) found it preferable to separate strains on

the basis of mild or severe symptoms on the wheat cultivar Michigan Amber. There is a strain variation in molecular weight of the capsid protein. The Type strain, McKinney's mild Ac85 strain, and one other have capsid proteins about 1000 d larger than that of 13 other isolates tested (M.K. Brakke, unpublished). No attempt yet has been made to correlate this capsid protein difference with other properties that might distinguish strains. Yield loss may be one property distinguishing strains, because fields observed to have equally high incidence and similar severity in early spring do not always have similar yield loss.

The host range of WSMV includes rye, oat, barley, wheat, maize, foxtail millets, and many grasses (Brakke, 1971a; Sill and Agusiobo, 1955). The host range of the mite vector, *E. tulipae*, includes the same crop plants, as well as sorghum and a number of grasses that only partially overlap those that are hosts of the virus (Connin, 1956; Slykhuis, 1955; Staples and Allington, 1956). Symptoms of WSMV are typical mosaic and stunting, which may be severe enough that plants do not head out.

WSMV occurs in North America, Romania, Yugoslavia, Russia, and Jordan (Slykhuis, 1967).

WSMV is identified by serology, electron microscopy, or presence of typical symptoms at 25 to 30° C following sap transmission. Antisera for identification may be produced to either the virion or to the 66 000 d protein.

8D–7.3 Soilborne Wheat Mosaic Virus

The SBWMV has two genomic single-stranded RNAs, components I and II, encapsidated in stiff, hollow rods 20 nm in diameter (Brakke, 1971b; Tsuchizaki et al., 1975). The larger RNA, component I, has 6500 bases in a rod 280 nm long sedimenting at 219 s (Brakke, 1977). It is always present, usually about 5% by weight as much as RNA II, but sometimes less and at times barely detectable. The smaller RNA, component II, has virions sedimenting at 177 s that are about 140 nm long with 3500 bases in the wild type. However, RNA II mutates readily by deletion. Mutant RNAs down to 2450 bases are infectious in combination with RNA I. As plants grow, mutants accumulate, with the frequency distribution of length of mutants varying from plant to plant. Some of the mutants cause more severe symptoms than wild type (Shirako and Brakke, 1984a, 1984b).

Loss due to SBWMV varies from 0 to 50% from year to year and from field to field. The variability in yield loss may result in part from infection by different strains of the virus. Early results indicated that strains of the virus might be distinguished by the size of component II RNA or the lengths of the rods encapsidating that RNA (Tsuchizaki et al., 1973; Brakke, 1977). However, the discovery that component II RNA mutates often, and that the frequency distribution of rod length varies from month to month for virions from a single plant (Shirako and Brakke, 1984b), necessitates a re-examination of the properties of strains of this

virus. The host range of the virus includes maize, rye, barley, wheat, some *Bromus* spp., and several species of Chenopodiaceae. Japanese strains infect *Nicotiana tabacum* L., but those from North America do not (Tsuchizaki et al., 1973).

SBWMV occurs in moderate concentration, 100 to 500 μg per gram of leaf and is readily identified by serology, electron microscopy, or by molecular weight of the capsid proteins, 20 000 d. SBWMV is sap transmissible, but usually fewer than half of the inoculated plants become infected. Deletion mutants may be more readily transmissible than wild type, but with too much deletion, transmissibility is lost.

The SBWMV gives a milder mosaic than WSMV. Optimum temperature for symptoms is 15° C. Mosaic at 25° C is very mild. Symptoms in the field usually disappear late in the spring as temperatures become warmer and plants larger. Infected plants are always stunted, by 20 to 30%, but some old cultivars of soft red winter wheat showed an extreme stunting, the rosette reaction, in which plants remained only a few centimeters tall. A new germplasm called Rosette shows this reaction and may be useful in distinguishing SBWMV from WSSMV (Patterson et al., 1983).

The SBWMV occurs in hard red winter and soft red winter wheat areas of the USA and in Brazil, France, Italy, and Japan. Resistance to SBWMV has been an essential ingredient of soft red winter wheats in the USA since the 1920s, and has become important since the 1960s for hard red winter wheats in eastern Nebraska, Kansas, and Oklahoma.

Resistant cultivars are available for both soft and hard red winter wheats. These resistant cultivars seldom show symptoms, suffer no detectable yield loss, and have no detectable virus in leaves or stems when they are grown in infested soil. And yet these same cultivars are fully susceptible to the virus by sap inoculation (McKinney, 1948) and at least some are hosts for the vector *P. graminis* (W.C. Langenberg, University of Nebraska, personal communication, 1983). At least one of these resistant cultivars, Homestead, suffers a much larger reduction in root mass after infection by sap inoculation than does the susceptible cultivar Scout, 66% reduction vs. 22%, respectively (H. Larsen et al., 1985). The response of cv. Newton was similar to that of Homestead. Clearly, in this and similar cultivars, resistance to SBWMV must involve some type of escape from systemic infection and not immunity, tolerance, or resistance to the vector. Since these other types of resistance may exist, it is perhaps not surprising that reports differ on the number of genes involved in resistance. Dubey et al. (1970) reported that resistance in soft red winter wheats was conditioned by three alleles at one locus, with the allele conditioning susceptibility to mosaic only being dominant over the allele conditioning susceptibility to the mosaic-rosette reaction; the third allele was dominant over the allele conditioning susceptibility to mosaic only. Modawi et al. (1982) reported that, for the hard red winter wheats, resistance was dominant and controlled by genes at a single locus. Earlier Shaalan et al.

(1966) implicated two factors, one partially dominant gene and one modifying. In Japanese cultivars, Mujake (1938) found evidence for one dominant gene for resistance and Nakagawa et al. (1959) found evidence for multiple alleles at three loci. Merkle and Smith (1983) reported one dominant resistance gene common to cultivars Homestead, Arthur, and Tascosa and a different dominant gene in Newton.

8D–7.4 Wheat Yellow Mosaic Virus

Wheat spindle streak mosaic (WSSMV) and WYMV have similar properties and are serologically closely related but not identical. The WSSMV should be considered a strain of WYMV, which was described first (Usugi and Saito, 1979). In the first edition of this monograph, WSSMV was called Ontario soilborne wheat mosaic (McKinney, 1967).

The WYMV has flexuous rods about 15 nm in diameter and varying in length from 200 to 2000 nm and more (Haufler and Fulbright, 1983; Slykhuis, 1976; Usugi and Saito, 1979). The range in length probably results largely from aggregation or breakdown, but it has been difficult to determine which. However, Usugi and Saito (1976) reported two zones when purified WYMV was centrifuged through a sucrose gradient. The upper zone, which had low infectivity, had rods 200 to 300 nm long and the lower, highly infectious zone had rods about 600 nm long. Slykhuis and Polak (1971) reported a high frequency of rods of 275 to 300 nm and 600 to 625 nm for WSSMV. More typical are the results of Haufler and Fulbright (1983), who found an average length of 1775 nm.

WSSMV is present in low concentration, which has made both purification and identification difficult (Slykhuis and Polak, 1971). Only a few rods are observed in 15 to 20 grid openings by electron microscopy of leaf dips, whereas a few rods of WSMV are observed in each grid opening. Rods of WSMV and WSSMV appear similar in electron microscopy, except that those of WSMV are more uniform in length.

The most successful purification of WYMV and WSSMV was reported by Usugi and Saito (1976; 1979). They reported a buoyant density in CsCl of 1.281 and a corrected A280/A260 ratio of 0.88, similar to that of other rod-shaped viruses. No information on the virus nucleic acid or capsid protein has been published. Antisera to the WSSMV and WYMV have been prepared (Usugi and Saito, 1979). The most practical serological test for identification appears to be adsorption of virus on antiserum coated specimen grids followed by antibody decoration and electron microscopy (Haufler and Fulbright, 1983).

WSSMV requires temperatures below 17° C for symptom expression with an optimum temperature of 10°C (Slykhuis, 1974). Symptoms include chlorotic to necrotic spindle-shaped streaks on leaves, stunting, reduced tillering, and reduced yields (Slykhuis, 1976). Symptoms develop on spring growth of winter wheat and have not been reported on spring wheat. WSSMV has not been reported to infect any plant besides wheat, although soilborne viruses of similar morphology are found on oats, bar-

ley, and rice (Hibino et al., 1981). WSSMV and/or WYMV occurs in Ontario, Canada; in the northeastern USA as far south as Kentucky (Williams et al., 1975) and as far west as Nebraska (Brakke, et al., 1982); and in India (Analwat et al., 1976), France (Signoret et al., 1977), and Japan (Usugi and Saito, 1979). It is probable that some of the disease attributed to SBWMV in the past has been due to WSSMV or to a mixture of WSSMV and SBWMV. When the two viruses are present together, the presence of WSSMV can easily go undetected.

8D–7.5 Other Viruses

Several leafhopper and planthopper transmitted viruses have been reported on wheat (Wiese, 1977). An additional leafhopper transmitted rhabdovirus, cereal chlorotic mottle virus, has been reported from Australia since Wiese wrote his monograph (Greber, 1982). These viruses are not sap transmissible; they usually cause severe symptoms on infected plants, but occur too sporadically to cause economic loss (Wiese, 1977). Exceptions are cereal streak in parts of Africa, wheat or cardamon mosaic streak in India, enanismo in Colombia and Ecuador, wheat dwarf in Czechoslovakia, and winter wheat mosaic in Russia which can all cause economic losses (Jackson et al., 1981; Harder and Bakker, 1973; Wiese, 1977; Slykhuis, 1967).

Wheat dwarf virus is a DNA-containing virus of the gemini group (Lindsten et al., 1981). Two other gemini viruses infect wheat, maize streak in Africa and chloris striate mosaic in Australia (also called Australian wheat striate mosaic) (Bock, 1974; Francki and Hatta, 1980).

There are three viruses similar to WSMV, namely Agropyron mosaic, Hordeum mosaic, and ryegrass mosaic, all of which infect wheat experimentally, and one of which, Agropyron mosaic, regularly infects wheat in Ontario and occasionally in England to cause a mild mosaic (Slykhuis, 1967, 1973; Plumb and Lennon, 1981). These viruses are not transmitted by *E. tulipae*, but Agropyron mosaic is transmitted by *Abacarus hystrix* (Mulligan, 1960). Another agent, wheat spot mosaic, is transmitted by *E. tulipae* but is not sap transmissible (Slykhuis, 1955). While this disease is readily found in hard red winter wheat areas of North America, no systematic studies have been done to determine its frequency or what losses it might cause. The causative agent or virus has not been identified.

Viruses of the potato Y group (potyviruses) cause serious diseases in almost every crop except small grains. One of these, maize dwarf mosaic virus (MDMV), has been found in wheat in New York (Boothroyd and Romaine, 1971). In view of the many strains of potyviruses and the widespread distribution of their vectors (aphids), it would not be surprising to find one of these viruses widespread in wheat in the future. In the late 1950s, no manually transmissible viruses (which includes MDMV) could be recovered from maize plots near the campus in Lincoln, NE (W.B. Allington, unpublished results). In the late 1970s, 100% of randomly sampled plants from the same plots had MDMV in late August

(R. Samson and M.K. Brakke, unpublished results). A similar change could occur in wheat.

Several viruses that have been transmitted to wheat in the laboratory occur commonly on other crops or weeds but rarely on wheat in the field. These include tobacco mosaic, cucumber mosaic, maize chlorotic mottle, and cocksfoot mottle virus. Barley stripe mosaic virus has been found on wheat in Mexico, Israel, and China (P. Burnett, R.G. Timian, and W.G. Langenberg, personal communication). Another virus, brome mosaic virus, is common on *Bromus inermis* but not on wheat in North America, and is found on grasses and occasionally on wheat in Europe (Lane, 1981). However, in South Africa, brome mosaic virus is reported to be common in wheat as part of a disease complex including BYDV, African cereal streak virus, and other viruses. Presumably, an efficient vector is present in South Africa but not in North America. Experimental transmission of brome mosaic virus in South Africa by aphids, leaf rust, and stem rust and through seed has been reported (Erasmus and Von Wechmar, 1983; Erasmus et al., 1983; Von Wechmar and Rybicki, 1985). Beetles transmit other members of the bromovirus group and the best evidence now suggests that they are vectors of brome mosaic virus (Lane, 1981). Full explanation of the epidemiology of brome mosaic virus in South Africa and elsewhere needs additional tests of vectors under laboratory and field conditions.

In the first edition of this monograph, aster yellows was included among the virus diseases. Since then, it has been discovered that aster yellows is caused by a mycoplasma, a bacteria-like microorganism lacking a cell wall (Doi et al., 1967).

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REFERENCES

A'Brook, J. 1974. Barley yellow dwarf virus: What sort of problem? Ann. Appl. Biol. 77:92–96.

----. 1981a. Forecasting the flight peaks of aphid vectors of cereal viruses. p. 67–72. *In* R.T. Plumb (ed.) Proc. 3rd Conf. Virus Diseases of Gramineae in Europe. 28–30 May 1980. Rothamsted Agric. Exp. Stn., Harpenden, Herts, U.K.

----. 1981b. Vectors of barley yellow dwarf virus. p. 21. *In* L.R. Taylor (ed.) Euraphid: Rothamsted 1980. Rothamsted Agric. Exp. Stn., Harpenden, Herts, U.K.

Adlakha, K.L., and L.M. Joshi, 1974. Black point of wheat. Ind. Phytopathol. 27:41–44.

----, and S.P. Raychaudhuri. 1975. Interaction between Helminthosporium sativum and wheat mosaic streak virus. Zeit. Pflanzenkrank. Pflanzenschutz. 82:201–206.

Ajayi, O., and A.M. Dewar. 1983. The effects of barley yellow dwarf virus, aphids and honeydew on *Cladosporium* infection of winter wheat and barley. Ann. Appl. Biol. 102:57–65.

Allan, R.E., R.F. Line, C.J. Peterson, Jr., G.L. Rubenthaler, K.J. Morrison, and C.R. Rohde. 1983. Crew, a multiline wheat cultivar. Crop Sci. 23:1015–1016.

Allen, R.F. 1923. A cytological study of infection of Baart and Kanred wheats by *Puccinia graminis tritici*. J. Agric. Res. 23:131–151.

----, 1926. A cytological study of *Puccinia triticina* physiologic form 11 on Little Club wheat. J. Agric. Res. 33:201–222.

----, 1928. A cytological study of *Puccinia glumarum* on *Bromus marginatus* and *Triticum vulgare*. J. Agric. Res. 36:487–513.

Analwat, Y.S., A. Majumdar, and V.V. Chenulu. 1976. First record of wheat spindle streak mosaic in India. Plant Dis. Rep. 60:782–783.

Andrews, C.J., and Y.C. Paliwal. 1983. The influence of preinfection cold hardening and disease development period on the interaction between barley yellow dwarf virus and cold stress tolerance in wheat. Can. J. Bot. 61:1935–1940.

Arthur, J.C. 1929. The plant rusts (Uredinales). John Wiley and Sons, New York.

Atkinson, T.G., and J.T. Slykhuis. 1963. Relation of spring drought, summer rains, and high fall temperatures to the wheat streak mosaic epiphytotic in southern Alberta, 1963. Can. Plant Dis. Surv. 43:154–159.

Babadoost, M., and T.T. Hebert. 1984. Incidence of *Septoria nodorum* in wheat seed and its effect on plant growth and grain yield. Plant Dis. 68:125–129.

Bailey, J.E., J.L. Lockwood, and M.V. Wiese. 1982. Infection of wheat by *Cephalosporium gramineum* as influenced by freezing of roots. Phytopathology 72:1324–1328.

Baker, K.F., and W.C. Snyder. 1965. Ecology of soil-borne plant pathogens: Prelude to biological control. University of California Press, Berkeley.

Bannon, E. 1978. A method of detecting *Septoria nodorum* on symptomless leaves of wheat. Ir. J. Agric. Res. 17:323–325.

Barr, D.J.S. 1981. *Polymyxa graminis*. Fungi Canadenses 199. National Mycological Herbarium, Agriculture Canada, Ottawa.

Batts, C.C.V. 1955. Observations on the infection of wheat by loose smut (*Ustilago tritici* (Pers.) Rostr.). Trans. Br. Mycol. Soc. 38:465–475.

Baxter, R.I., and C.D. Blake. 1968. *Pratylenchus thornei*—a cause of root necrosis in wheat. Nematologia 14:351–361.

Bedi, S.K.S. 1957. Further studies on the control of loose smut of wheat in the Punjab. Ind. Phytopathol. 10:133–137.

Benedict, W.G., and W.B. Mountain. 1956. Studies on the etiology of a root rot of winter wheat in Southwestern Ontario. Can. J. Bot. 34:159–174.

Bent, K.J. 1978. Chemical control of powdery mildews. p. 259–282. *In* D.M. Spencer (ed.) The powdery mildews. Academic Press, London.

Bever, W.M. 1937. Influence of stripe rust on growth, water economy and yield of wheat and barley. J. Agric. Res. 54:375–385.

----, and J.W. Pendleton. 1954. The effect of soil-borne wheat mosaic on yield of winter wheat. Plant Dis. Rep. 38:266–267.

Bhowmik, T.P. 1969. *Alternaria* seed infection of wheat. Plant Dis. Rep. 53:77–80.

Biffen, R.H. 1905. Mendel's law of inheritance and wheat breeding. J. Agric. Sci. 1:4–48.

Bird, A.F. 1981. The *Anguina–Corynebacterium* association. p. 303–323. *In* B.M. Zuckerman and R.A. Rohde (ed.) Plant parasitic nematodes, Vol. 3. Academic Press, New York.

Bock, K.R. 1974. Maize streak virus. C.M.I./A.A.B. descriptions of plant viruses 133. Commonwealth Mycological Institute, Surrey, U.K.

Bockus, W.W. 1983. Effects of fall infection by *Gaeumannomyces graminis* var. *tritici* and triadimenol seed treatment on severity of take-all in winter wheat. Phytophathology 73:540–543.

----, and M.M. Claassen, 1985. Effect of lime and sulfur application to low-pH soil on incidence of Cephalosporium stripe in winter wheat. Plant Dis. 69:576–578.

----, J.P. O'Conner and P.J. Raymond. 1983. Effect of residue management method on incidence of Cephalsporium stripe under continuous winter wheat production. Plant Dis. 67:1323–1324.

----, and T. Sim IV. 1982. Quantifying Cephalosporium stripe disease severity on winter wheat. Phytopathology 72:493–495.

Boewe, G.H. 1960. Diseases of wheat, oats, barley, and rye. Illinois Nat. Hist. Surv. Circ. 48.

Boothroyd, C.W., and C.P. Romaine. 1971. Winter wheat as a reservoir for maize dwarf mosaic virus. Phytopathology 61:885–886.

Brakke, M.K. 1971a. Wheat streak mosaic virus. C.M.I./A.A.B. descriptions of plant viruses 48. Commonwealth Mycological Institute, Surrey, U.K.

----. 1971b. Soil-borne wheat mosaic virus. C.M.I./A.A.B. descriptions of plant viruses 77. Commonwealth Mycological Institute, Surrey, U.K.

----. 1977. Sedimentation coefficients of the virions of soil-borne wheat mosaic virus. Phytopathology 67:1433–1438.

----, E.M. Ball, Y.H. Hsu, and W.G. Langenberg. 1986. Wheat streak mosaic virus cylindrical inclusion body protein. J. Gen. Virology 68: In press.

----, A.P. Estes, and M.L. Schuster. 1965. Transmission of soil-borne wheat mosaic virus. Phytopathology 55:79–86.

----, W.G. Langenberg, and R.G. Samson. 1982. Wheat spindle streak mosaic virus in Nebraska. Plant Dis. 66:958–959.

Bretag, T.W., and P.R. Merriman. 1981. Epidemiology and cross-infection of *Claviceps purpurea*. Trans. Br. Mycol. Soc. 77:211–213.

Briggle, L.W. 1969. Near-isogenic lines of wheat with genes for resistance to *Erysiphe graminis* f. sp. *tritici*. Crop Sci. 9:70–72.

----. 1984. Barley yellow dwarf virus (BYDV) workshop sponsored by UNOP and CIMMYT in 1983. Annu. Wheat News. 30:16–17.

----, and L.P. Reitz. 1963. Classification of *Triticum* species and of wheat varieties grown in the United States. USDA Tech. Bull. 1278. U.S. Government Printing Office, Washington, DC.

Broscious, S.C., J.A. Frank, and J.R. Frederick. 1985. Influence of winter wheat management practices on the severity of powdery mildew and Septoria blotch in Pennsylvania. Phytopathology 75:538–542.

Browder, L.F. 1971. Pathogenic specialization in cereal rust fungi, especially *Puccinia recondita* f. sp. *tritici*: Concepts, methods of study, and application. USDA–ARS Tech. Bull. 1432. U.S. Government Printing Office, Washington, DC.

----. 1980. A compendium of information about named genes for low reaction to *Puccinia recondita* in wheat. Crop Sci. 20:775–779.

Brown, J.K., S.D. Wyatt, and D. Hazelwood. 1984. Irrigated corn as a source of barley yellow dwarf virus and vector in eastern Washington. Phytopathology 74:46–49.

Browning, J.A., and K.J. Frey. 1969. Multiline cultivars as a means of disease control. Annu. Rev. Phytopathol. 7:355–382.

Bruehl, G.W. 1951a. *Rhizoctonia solani* in relation to cereal crown and root rots. Phytopathology 41:375–377.

----. 1951b. Root rot in cereals and grasses. South Dak. Farm Home Res. 2:76–79.

----. 1953. Pythium root rot of barley and wheat. USDA Tech. Bull. 1084. U.S. Government Printing Office, Washington, D.C.

----. 1961. Barley yellow dwarf. Monogr. No. 1. American Phytopathological Society, St. Paul.

----. 1967. Diseases other than rust, smut, and virus. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:375–410.

----. 1968. Ecology of Cephalosporium stripe disease of winter wheat in Washington. Plant Dis. Rep. 52:590–594.

----. 1975. Biology and control of soil-borne plant pathogens. American Phytopathological Society, St. Paul.

----, and P. Lai. 1968. Influence of soil pH and humidity on survival of *Cephalosporium gramineum* in infested wheat straw. Can. J. Plant Sci. 48:245–252.

----, C.J. Peterson, Jr., and R. Machtmes. 1974. Influence of seeding date, resistance, and benomyl on Cercosporella foot rot of winter wheat. Plant Dis. Rep. 58:554–558.

Burnett, P.A., and H.C. Smith. 1976. Where have all the aphids gone? Crop Res. News (N.Z. Dep. Sci. Ind. Res.) 3:14–15.

Bushnell, W.R. 1967. Symptom development in mildewed and rusted tissues. p. 21–39. *In* C.J. Mirocha and I. Uritani (ed.) The dynamic role of molecular constituents in plant-parasite interaction. American Phytopathological Society, St. Paul.

----. 1984. Structural and physiological alterations in susceptible host tissue. p. 477–507. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

----, and P.J. Allen. 1962. Respiratory changes in barley leaves produced by single colonies of powdery mildew. Plant Physiol. 37:751–758.

----, and J. Gay. 1978. Accumulation of solutes in relation to the structure and function of haustoria in powdery mildews. p. 183–235. *In* D.M. Spencer (ed.) The powdery mildews. Academic Press. London.

Butler, F.C. 1961. Root and foot rot diseases of wheat. N.S.W. Dep. Agric. Sci. Bull. 77.

Caldwell, R.M., L.E. Compton, J.F. Schafer, and F.L. Patterson. 1954. Knox, a new leaf rust resistant and stem rust escaping soft winter wheat. Phytopathology 44:483–484. (Abstr.)

Campbell, L.G., E.G. Heyne, D.M. Gronau, and C. Niblett. 1975. Effect of soilborne wheat mosaic virus on wheat yield. Plant Dis. Rep. 59:472–476.

Cardiff, I.D., O.L. Waller, H.V. Carpenter, G.A. Olson, E.G. Schafer, and A.I. Sherman. 1914. Report on fires occurring in threshing separators in eastern Washington during the summer of 1914. Washington Agric. Exp. Stn. Bull. 117.

Carlson, R.R., and A.K. Vidaver. 1982a. Bacterial mosaic, a new corynebacterial disease of wheat. Plant Dis. 66:76–79.

----, and ----. 1982b. Taxonomy of *Corynebacterium* plant pathogens, including a new pathogen of wheat, based on polyacrylamide gel electrophoresis of cellular proteins. Int. J. Syst. Bacteriol. 32:315–326.

Carrigan, L.L., H.W. Ohm, J.E. Foster, and F.L. Patterson. 1981. Response of winter wheat cultivars to barley yellow dwarf virus infection. Crop Sci. 21:377–380.

Carroll, T.W., S.K. Zaske, R.H. Brlansky. 1982. Separation of Montana isolates of wheat streak mosaic virus on Michigan Amber wheat. Plant Dis. 66:916–918.

Carver, T.L.W., and W.R. Bushnell. 1983. The probable role of primary germ tubes in water uptake before infection by *Erysiphe graminis*. Physiol. Plant Pathol. 23:229–240.

Chester, K.S. 1946. The nature and prevention of the cereal rusts as exemplified in the leaf rust of wheat. Chronica Botanica, Waltham, MA.

Chinn, S.H.F. 1978. Influence of seed treatment with imazalil on common root rot and the size of the subcrown internode of wheat. Phytopathology 68:1662–1666.

Christensen, N.W., R.G. Taylor, T.L. Jackson, and B.L. Mitchell. 1981. Chloride effects on water potentials and yield of winter wheat infected with take-all root rot. Agron. J. 73:1053–1058.

Christie, J.R., and V.G. Perry. 1951. A root disease of plants caused by a nematode of the genus *Trichodorus*. Science 113:491–493.

CIMMYT. (No date.) A Proposal for a technical assistance grant for a research programme on the control of barley yellow dwarf disease of cereal crops to be undertaken by the International Maize and Wheat Improvement Center (CIMMYT). CIMMYT, Mexico. (n.d.)

CIMMYT. 1977. Field manual of common wheat diseases and pests. CIMMYT Inf. Bull. 29.

Cisar, G., C.M. Brown, and H. Jedlinski. 1982a. Diallel analyses for tolerance in winter wheat to the barley yellow dwarf virus. Crop Sci. 22:328–333.

----, ----, and ----. 1982b. Effect of fall or spring infection and sources of tolerance of barley yellow dwarf of winter wheat. Crop. Sci. 22:474–478.

Clark, M.F., and A.N. Adams. 1977. Characteristics of the microplate method of enzyme-linked immunosorbant assay for the detection of plant viruses. J. Gen. Virology 34:475–483.

Coakley, S.M., R.F. Line, and W.S. Boyd. 1983. Regional models for predicting stripe rust on winter wheat in the Pacific Northwest. Phytopathology 73:1382–1385.

Cobb, N.A. 1890, 1892, 1894. Contributions to an economic knowledge of Australian rusts (Uredineae). Agric. Gaz. N.S.W. 1:185–214, 3:44–48, 181–212, 5:239–250.

Conners, I.L. 1954. The organism causing dwarf bunt of wheat. Can. J. Bot. 32:426–431.

Connin, R.V. 1956. The host range of the wheat curl mite, vector of wheat streak mosaic. J. Econ. Entomol. 49:1–4.

Cook, R.J. 1980. Fusarium foot rot of wheat and its control in the Pacific Northwest. Plant Dis. 64:1061–1066.

----. 1981. The influence of rotation crops on take-all decline phenomenon. Phytopathology 71:189–192.

----, and K.F. Baker. 1983. The nature and practice of biological control of plant pathogens. American Phytopathological Society, St. Paul.

----, and W.A. Haglund. 1982. Pythium root rot: A barrier to yield of Pacific Northwest wheat. Agric. Res. Ctr. Res. Bull. XB0913. Washington State University, Pullman.

----, J.W. Sitton, and J.T. Waldher. 1980. Evidence for *Pythium* as a pathogen of direct-drilled wheat in the Pacific Northwest. Plant Dis. 64:102–103.

Cooper, P. 1977. Grass viruses in Northern Ireland. Ann. Phytopathol. 9:261–266.

Creatura, P.J., G.R. Safir, and R.P. Scheffer. 1981. Effects on *Cephalosporium gramineum* and a toxic metabolite on stomatal conductance of wheat. Physiol. Plant Pathol. 19:313–323.

Cummins, G.B. 1971. The rust fungi of cereals, grasses, and bamboos. Springer-Verlag New York, New York.

----, and Y. Hiratsuka. 1983. Illustrated genera of rust fungi. Rev. ed. American Phytopathological Society, St. Paul.

Cunfer, B.M. 1975. Colonization of ergot honeydew by *Fusarium heterosporum*. Phytopathology 65:1372–1374.

----. 1978. The incidence of *Septoria nodorum* in wheat seed. Phytopathology 68:832–835.

----. 1983. Epidemiology and control of seed-borne *Septoria nodorum* on wheat. Seed Sci. Technol. 11:707–718.

----, D.E. Mathre, and E.A. Hockett. 1975. Factors influencing the susceptibility of male-sterile barley to ergot. Crop Sci. 15:194–196.

----, and B.L. Scolari. 1982. *Xanthomonas campestris* pv. *translucens* on triticale and other small grains. Phytopathology 72:683–686.

----, and A. Seckinger. 1977. Survival of *Claviceps purpurea* and *C. paspali* sclerotia. Mycologia 69:1142–1148.

d'Arcy, C.J., A.D. Hewings, P.A. Burnett, and H. Jedlinski. 1983. Comparative purification of two luteoviruses. Phytopathology 73:755–759.

Darlington, L.C., and D.E. Mathre. 1976. Resistance of male sterile wheat to ergot as related to pollination and host genotype. Crop Sci. 16:728–730.

Dedryver, C.A., and Y. Robert. 1981. Ecological role of maize and cereal volunteers as reservoirs for gramineae virus transmitting aphids. p. 61–66. *In* R.T. Plumb (ed.) Proc. 3rd Conference on Virus Diseases of Gramineae in Europe. Rothamsted Agric. Exp. Stn., Harpenden, Herts. U.K.

Dickson, J.G. 1956. Diseases of field crops. 2nd ed. McGraw-Hill, New York.

Diehl, J.A., R.D. Tinline, R.A. Kochmann, P.J. Shipton, and A.D. Rovira. 1982. The effect of fallow periods on common root rot of wheat in Rio Grande do Sul, Brazil. Phytopathology 72:1297–1301.

Doi, Y., M. Teranaka, K. Yora, and H. Asuyamo. 1967. Mycoplasma or PLT group-like microorganisms found in phloem elements of plants infected with mulberry dwarf, potato witches' broom, aster yellows, or Paulownia witches' broom. Ann. Phytopathol. Soc. Jpn. 33:259–266.

Dolezal, W.E., and J.P. Jones, 1981. Fungicide promising for take-all in wheat. Agrichemical Age 23:34.

Doling, D.A., and J.K. Doodson. 1968. The effect of yellow rust on the yield of spring and winter wheat. Trans. Br. Mycol. Soc. 51:427–434.

Doodson, J.K. 1967. A survey of barley yellow dwarf virus in S.24 perennial ryegrass in England and Wales, 1966. Plant Pathol. 16:42–45.

----. 1982. Disease testing at NIAB, Britain's unique agricultural institute. Plant Dis. 66:875–879.

Dubey, S.N., C.M. Brown, and L.L. Hooker. 1970. Inheritance of field reaction to soil-borne wheat mosaic virus. Crop Sci. 10:93–95.

Dubin, H.J., and E. Torres. 1981. Causes and consequences of the 1976–1977 wheat leaf rust epidemic in northwest Mexico. Annu. Rev. Phytopathol. 19:41–49.

Duran, R. 1973. Ustilaginales. p. 281–300. *In* G.C. Ainsworth et al. (ed.) The fungi: An advanced treatise, Vol. 4B. Academic Press, New York.

----, and G.W. Fischer. 1961. The genus *Tilletia*. Washington State University, Pullman.

Durbin, R.D. 1984. Effects of rust on plant development in relation to the translocation of inorganic and organic solutes. p. 509–528. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

Dyck, P.L., and E.R. Kerber. 1985. Resistance of the race-specific type. p. 465–496. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Dye, D.W., J.F. Bradbury, M. Goto, A.C. Hayward, R.A. Lelliott, and M.N. Schroth. 1980. International standards for naming pathovars of phytopathogenic bacteria and a list of pathovar names and pathotype strains. Rev. Plant Pathol. 59:153–158.

Ehrlich, H.G., and M.A. Ehrlich. 1963. Electron microscopy of the host–parasite relationships in stem rust of wheat. Am. J. Bot. 50:123–130.

Ellingboe, A.H. 1978. A genetic analysis of host–parasite interactions. p. 159–181. *In* D.M. Spencer (ed.) The powdery mildews. Academic Press, London.

Endo, B.Y. 1959. Responses of the root-lesion nematodes, *Pratylenchus brachyurus* and *P. zeae*, to various plants and soil types. Phytopathology 49:417–421.

Erasmus, D.S., and M.B. VonWechmar. 1983. The association of brome mosaic virus and wheat rusts. I. Transmission of BMV by uredospores of wheat stem and leaf rust. Phytopath. Z. 108:26–33.

----, E.P. Rybicki, and M.B. VonWechmar. 1983. The association of brome mosaic virus and wheat rusts. II. Detection of BMV in/on uredospores of wheat stem rust. Phytopathol. Z. 108:34–40.

Estes, A.P., and M.K. Brakke. 1966. Correlation of *Polymyxa graminis* with transmission of soil-borne wheat mosaic virus. Virology 28:772–774.

Eversmeyer, M.G., W.G. Willis, and C.L. Kramer. 1983. Effect of soil fumigation on occurrence and damage caused by soil-borne wheat mosaic. Plant Dis. 67:1000–1002.

Eyal, Z. 1981a. Integrated control of Septoria diseases of wheat. Plant Dis. 65:763–768.

----. 1981b. Research on Septoria leaf blotch: Recent advances. Bull. EPPO 11:53–57.

----, Z. Amiri, and I. Wahl. 1973. Physiologic specialization of *Septoria tritici*. Phytopathology 63:1087–1091.

Fargette, D., R.M. Lister, and E.L. Hood. 1982. Grasses as a reservoir of barley yellow dwarf virus in Indiana. Plant Dis. 66:1041–1045.

Farrer, W. 1898. Making and improvement of wheats for Australian conditions. Agric. Gaz. N.S.W. 9:131–168, 241–250.

Fellows, H., and J.W. Schmidt. 1953. Reaction of Agrotricum hybrids to the virus of yellow streak mosaic of wheat. Plant Dis. Rep. 37:349–51.

Fenster, C.R., M.G. Boosalis, and J.L. Weihing. 1972. Date of planting studies of winter

wheat and winter barley in relation to root and crown rot, grain yields and quality. Nebraska Agric. Exp. Stn. Res. Bull. 250.

Fernandez, J.A., R. Duran, and J.F. Schafer. 1978. Histological aspects of dwarf bunt resistance in wheat. Phytopathology 68:1417–11421.

Fischer, G.W. 1953. Manual of the North American smut fungi. Ronald Press, New York.

----, and C.S. Holton. 1957. Biology and control of the smut fungi. Ronald Press, New York.

Fitzgerald, P.J., and W.N. Stoner. 1967. Barley yellow dwarf studies in wheat (*Triticum aestivum* L.). I. Yield and quality of hard red winter wheat infected with barley yellow dwarf virus. Crop Sci. 7:337–341.

Flentje, N.T. 1957. Studies on *Pellicularia filamentosa* (Pat.) Rogers. III. Host penetration and resistance, and strain specialization. Trans. Br. Mycol. Soc. 40:322–336.

Flor, H.H. 1932. Heterothallism and hybridization in *Tilletia tritici* and *T. levis*. J. Agric. Res. 44:49–58.

----. 1971. Current status of the gene-for-gene concept. Annu. Rev. Phytopathol. 9:275–296.

Fontana, F. 1767. Observations on the rust of grain. Transl. from Italian by P.P. Pirone. Phytopathol. classics no. 2. American Phytopathological Society, St. Paul. (1932).

Forrer, H.R., F.H. Rijskijk, and J.C. Zadoks. 1982. Can mildew assist in the entry of Fusarium fungi into wheat? Neth. J. Plant Pathol. 88:123–125.

Francis, R.G., and L.W. Burgess. 1977. Characteristics of two populations of *Fusarium roseum* 'Graminearum' in eastern Australia. Trans. Br. Mycol. Soc. 68:421–427.

Francki, R.I.B., and T. Hatta. 1980. Chloris striate mosaic virus. C.M.I./A.A.B. descriptions of plant viruses 221. Commonwealth Mycological institute, Surrey, U.K.

Fryda, S.J., and J.D. Otta. 1978. Epiphytic movement and survival of *Pseudomonas syringae* on spring wheat. Phytopathology 68:1064–1067.

Fulling, E.H. 1943. Plant life and the law of man. IV. Barberry, currant and gooseberry, and cedar control. Bot. Rev. 9:483–592.

Gallun, R.L. 1965. Hessian fly—How to control it. USDA Leaflet 533. U.S. Government Printing Office. Washington, D.C.

Gaskin, T.A., and J.F. Schafer. 1962. Some histological and genetic relationships of resistance of wheat to loose smut. Phytopathology 52:602–607.

Gates, L.F. 1969. Incidence and effect of wheat spindle streak mosaic in Essex and Kent Counties, Ontario, 1967–68. Can. Plant Dis. Surv. 49:58–59.

Gaunt, R.E. 1981. Disease tolerance—An indicator of thresholds? Phytopathology 71:915–916.

Gerdeman, J.W., and R.O. Wiebel. 1960. Cephalosporium stripe on small grains in Illinois. Plant Dis. Rep. 44:877.

Gill, C.C. 1967. Susceptibility of common and durum spring wheats to barley yellow dwarf virus. Can. J. Plant Sci. 47:571–576.

----. 1980. Assessment of losses on spring wheat naturally infected with barley yellow dwarf virus. Plant Dis. 64:197–203.

----, P.H. Westdal, and H.P. Richardson. 1969. Comparison of aster yellows and barley yellow dwarf on wheat and oats. Phytopathology 59:527–531.

Gill, K.S., G.S. Nanda, H.S. Dhaliwal, and S.S. Aujla. 1983. Studies to breed for resistance against Karnal bunt disease (*Neovossia indica*) in wheat. p. 793–799. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University, Kyoto.

Gordon, D.T., O.E. Bradfute, R.E. Gingery, J.K. Knoke, R. Louie, L.R. Nault, and G.E. Scott. 1981. Introduction: Geographical distribution, pathogen characteristics, and economic importance. P. 1–12. *In* D.T. Gordon et al. (ed.) Virus and virus-like diseases of maize in the United States. Southern Coop. Ser. Bull. 247. Ohio Agric. Res. Dev. Ctr., Wooster, OH.

Grafton, K.F., J.M. Poehlman, O.P. Sehgal, and D.T. Sechler. 1982. Tall fescue as a natural

host and aphid vectors of barley yellow dwarf virus in Missouri. Plant Dis. 66:318–320.

Greber, R.S. 1982. Cereal chlorotic mottle virus. C.M.I./A.A.B. description of plant viruses no. 251. Commonwealth Mycological Institute, Surrey, U.K.

Green, G.J., and A.B. Campbell. 1979. Wheat cultivars resistant to *Puccinia graminis tritici* in western Canada and their development, performance, and economic value. Can. J. Plant Pathol. 1:3–11.

Griffin, D.M. 1972. Ecology of soil fungi. Chapman and Hall, London.

Groth, J.V. 1976. Multilines and "super races": A simple model. Phytopathology 66:937–939.

Gupta, P., and G. Swarup. 1968. On the ear-cockle and yellow ear rot diseases of wheat. I. Symptoms and histopathology. Ind. Phytopathol. 21:318–324.

----, and ----. 1972. Ear-cockle and yellow ear-rot diseases of wheat. II. Nematode bacterial association. Nematologica 18:320–324.

Halstead, B.E., and C.C. Gill. 1971. Effect of inoculation of oats with paired combinations of barley yellow dwarf virus isolates. Can. J. Bot. 49:577–581.

Hamilton, L.M. 1939. Stem rust in the spring wheat area in 1878. Minnesota Hist. 20:156–164.

Harder, D.E., and W. Bakker. 1973. African cereal streak: A new disease of cereals in East Africa. Phytopathology 63:1407–1411.

----, and J. Chong. 1984. Structure and physiology of haustoria. p. 431–476. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

Harding, H., and R.D. Tinline. 1983. The existence of differentially fertile strains in two populations of *Cochliobolus sativus*. Can. J. Plant Pathol. 5:17–20.

Harvey, T.L., and R.W. Livers. 1975. Resistance to wheat curl mite, *Aceria tulipae* Keifer, in rye and wheat rye addition lines. Environ. Entomol. 4:523–526.

----, and T.J. Martin. 1980. Effects of wheat pubescence on infestations of wheat curl mite and incidence of wheat streak mosaic virus. J. Econ. Entomol. 73:225–227.

Haufler, K.Z., and D.W. Fulbright. 1983. Detection of wheat spindle streak mosaic virus by serologically specific electron microscopy. Plant Dis. 67:988–990.

Hendrix, J.W. 1967. Stripe rust of wheat. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:325–335.

Hermansen, J.E. 1968. Studies on the spread and survival of cereal rust and mildew diseases in Denmark. Friesia 8:161–359.

----, and A. Wiberg. 1972. On the appearance of *Erysiphe graminis* f. sp. *hordei* and *Puccinia hordei* in the Faeroes and the possible primary sources of inoculum. Friesia 10:30–34.

Herrman, T., and M.V. Wiese. 1985. Influence of cultural practices on incidence of foot rot in winter wheat. Plant Dis. 69:948–950.

Hibino, H., T. Usugi, and Y. Saito. 1981. Comparative electron microscopy of inclusions associated with five soil-borne filamentous viruses of cereals. Ann. Phytopathol. Soc. Jpn. 47:510–519.

Hill, J.P., J.A. Fernandez, and M.S. McShane. 1983. Fungi associated with common root rot of winter wheat in Colorado and Wyoming. Plant Dis. 67:795–797.

Hoffmann, J.A. 1971. Control of common and dwarf bunt of wheat by seed treatment with thiabendazole. Phytopathology 61:1071–1074.

----. 1982. Bunt of wheat. Plant Dis. 66:979–986.

----, and J.T. Waldher. 1981. Chemical seed treatments for controlling seedborne and soilborne common bunt of wheat. Plant Dis. 65:256–259.

Holland, J., K. Spindler, F. Horodyski, E. Grabau, S. Nichol, and S. VandePol. 1982. Rapid evolution of RNA genomes. Science 215:1577–1585.

Holmes, S.J.I. 1977. Ryegrass mosaic virus and barley yellow dwarf virus in the west of Scotland. Ann. Phytopathol. 9:287–292.

----, and J. Colhoun. 1974. Infection of wheat by *Septoria nodorum* and *S. tritici* in relation

to plant age, air temperature and relative humidity. Trans. Br. Mycol. Soc. 63:329–338.

Holton, C.S. 1967. Smuts. *In* S. Quisenbery and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:337–353.

----, and F.D. Heald. 1941. Bunt or stinking smut of wheat. Burgess Publishing Co., Minneapolis.

----, and L.H. Purdy, Jr. 1954. Control of soil-borne common bunt of winter wheat in the Pacific Northwest by seed treatment. Plant Dis. Rep. 38:753–754.

Hosford, R.M., Jr. 1971. A form of *Pyrenophora trichostoma* pathogenic to wheat and other grasses. Phytopathology 61:28–32.

----. 1972. Propagules of *Pyrenophora trichostoma*. Phytopathology 62:627–629.

----. 1975. *Phoma glomerata*, a new pathogen of wheat and triticale, cultivar response related to wet period. Phytopathology 65:1236–1239.

----. 1976. Fungal leaf spot diseases of wheat in North Dakota. N.D. Agric. Exp. Stn. Bull. 500.

----. 1982a. White blotch incited in wheat by *Bacillus megaterium* pv. *cerealis*. Phytopathology 72:1453–1459.

----. (ed.) 1982b. Proc. Tan spot of wheat and related diseases workshop. N.D. Agric. Exp. Stn.

----, and R.H. Busch. 1974. Losses in wheat caused by *Pyrenophora trichostoma* and *Leptosphaeria avenaria* f. sp. *triticea*. Phytopathology 64:184–187.

----, G.R.M. Solangi, and R.L. Kiesling. 1975. Inheritance in *Cochliobolus sativus*. Phytopathology 65:699–703.

How, S.H. 1963. Wheat streak mosaic virus on corn in Nebraska. Phytopathology 53:279–280.

Huber, D.M. 1981. Incidence and severity of take-all of wheat in Indiana. Plant Dis. 65:734–737.

----, G.C. Painter, H.C. Mckay, and D.L. Peterson, 1968. Effect of nitrogen fertilization on take-all of winter wheat. Phytopathology 58:1470–1472.

Huguelet, J.E., and R.L. Kiesling. 1973. Influence of inoculum composition on the black point disease of durum wheat. Phytopathology 63:1220–1225.

Jackson, A.O., G.M. Milbrath, and H. Jedlinski. 1981. Rhabdovirus diseases of the Gramineae. p. 51–76 *In* D.T. Gordon et al. (ed.) Virus and viruslike diseases of maize in the United States. Southern Coop. Ser. Bull. 247. Ohio Agric. Res. Dev. Ctr., Wooster, OH.

Jedlinski, H. 1972. Tolerance to two strains of barley yellow dwarf virus in oats. Plant Dis. Rep. 56:230–234.

----. 1981. Rice root aphid. *Rhopalosiphum rufiabdominalis*, a vector of barley yellow dwarf virus in Illinois and the disease complex. Plant Dis. 65:975–978.

----, and C.M. Brown. 1965. Cross protection and mutual exclusion by three strains of barley yellow dwarf virus in *Avena sativa* L. Virology 26:613–621.

Jeger, M.J. 1980. Multivariate models of the components of partial resistance. Prot. Ecol. 2:265–269.

----, E. Griffiths, and D.G. Jones. 1981. Disease progress of non-specialized fungal pathogens in intraspecific mixed stands of cereal cultivars. I. Models. Ann. Appl. Biol. 98:187–198.

----, ----, and ----. 1983a. Seasonal variation in the components of partial resistance of seedlings of winter wheat cultivars Maris Huntsman and Maris Ranger to *Septoria nodorum*. Plant Pathol. 32:187–195.

----, D.G. Jones, and E. Griffiths. 1983b. Components of partial resistance of wheat seedlings to *Septoria nodorum*. Euphyptica 32:575–584.

Jenkins, W.F., and D.P. Taylor. 1967. Plant nematology. Van Nostrand Reinhold Co., New York.

Jenkyn, J.F., and A. Bainbridge. 1978. Biology and pathology of cereal powdery mildews. p. 283–321. *In* D.M. Spencer (ed.) The powdery mildews. Academic Press, London.

Jensen, J.L. 1888. The propagation and prevention of smut in oats and barley. J. R. Agric. Soc. Engl. 24:4.

Jensen, S.G. 1969a. Occurrence of virus particles in the phloem tissue of BYDV infected barley. Virology 38:83–91.

----. 1969b. Composition and metabolism of barley leaves infected with barley yellow dwarf virus. Phytopathology 59:1694–1698.

----. 1973. Systemic movement of barley yellow dwarf virus in small grains. Phytopathology 63:854–856.

----, P.J. Fitzgerald, and J.R. Thysell. 1971. Physiology and field performance of wheat infected with barley yellow dwarf virus. Crop Sci. 11:775–780.

Johnson, R. 1984. A critical analysis of durable resistance. Annu. Rev. Phytopathol. 22:309–330.

Johnston, C.O. 1967. Leaf rust of wheat. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:317–325.

Johnston, R.H., and D.E. Mathre. 1972. Effect of infection by *Cephalosporium gramineum* on winter wheat. Crop Sci. 12:817–819.

Jones, D.G., and B.C. Clifford. 1984. Cereal diseases: Their pathology and control. 2nd ed. John Wiley and Sons, New York.

Jones, J.P., and F.C. Collins. 1971. Control of loose smut of wheat with carboxin and benomyl. Plant Dis. Rep. 55:1053–1055.

Joshi, L.M. 1980. The disease surveillance system for wheat in India. *In* H.C. Govindu et al. (ed.) Assessment of crop losses due to pests and diseases. Univ. Agric. Sci. Hebbal, Bangalore, Tech. Ser. 33:211–217.

----, D.V. Singh, K.D. Srivastava, and R.D. Wilcoxson. 1983. Karnal bunt: A minor disease that is now a threat to wheat. Bot. Rev. 49:309–330.

Junke, M.E., D.E. Mathre, and D.C. Sands. 1984. A selective medium for *Gaeumannomyces graminis* var. *tritici*. Plant Dis. 68:233–236.

Khan, T.N., W.J.R. Boyd, and W.P. Skoropad. 1971. The occurrence of *Drechslera tritici-repentis* on wheat in Western Australia and South Australia. J. Aust. Inst. Agric. Sci. 37:61–62.

Kim, H.K. 1983. Epidemiological, genetical, and physiological studies of the bacterial leaf streak pathogen *Xanthomonas campestris* pv. *translucens* (J.J.R.) Dowson. Ph.D. thesis. Montana State University, Bozeman. DA 43/07-B:2063.

King, J.E., R.J. Cook, and S.C. Melville. 1983. A review of Septoria diseases of wheat and barley. Ann. Appl. Biol. 103:345–373.

Kingsland, G.C. 1982. Triadimefon for control of powdery mildew of wheat. Plant Dis. 66:139–141.

Kislev, M.E. 1982. Stem rust of wheat 3300 years old found in Israel. Science 216:993–994.

Kline, D.M., and R.R. Nelson. 1971. The inheritance of factors in *Cochliobolus sativus* conditioning lesion induction on gramineous hosts. Phytopathology 61:1052–1054.

Koehler, B., W.M. Bever, and O.T. Bonnett. 1952. Soil-borne wheat mosaic. Illinois Agric. Exp. Stn. Bull. 556.

Krishna, A., and R.A. Singh. 1982. Taxonomy of Karnal bunt fungus: Evidence in support of genus Neovossia. Indian Phytopathol. 35:544–545.

Krüger, J., and G.M. Hoffmann. 1978. Differenzierung von *Septoria nodorum* Berk. und *Septoria avenae* Frank f. sp. *triticea* T. Johnson. Z. Pflanzenkr. Pflanzensch. 85:645–650.

Kucharek, T.A., and J.H. Walker. 1974. The presence of and damage caused by soil-borne wheat mosaic virus in Florida. Plant Dis. Rep. 58:763–765.

Lamey, H.A., and R.G. Timian. 1979. Wheat streak mosaic. N.D. State Univ. Coop. Ext. Serv. Circ pp-646.

Lane, L.C. 1981. Bromoviruses. p. 334–376. *In* E. Keerstak (ed.) Handbook of plant virus infections and comparative diagnosis. Elsevier/North Holland Biomedical Press, Amsterdam.

Larose, E., and R. Vanderwalle. 1937. Quelques résultats d'infection artificielle d'*Ustilago tritici* Schaff. sur le Froment. Bull. Inst. Agron. Stn. Rech. Gembloux 6:81–87.

Larson, H.J., M.K. Brakke, and W.G. Langenberg. 1985. Relationships between wheat streak mosaic virus and soilborne wheat mosaic virus infection, disease resistance, and early growth of winter wheat. Plant Dis. 69:857–862.

Larson, R.I., and T.G. Atkinson. 1973. Wheat–*Agropyron* chromosome substitution lines as sources of resistance to wheat streak mosaic virus and its vector, *Aceria tulipae*. p. 173–177. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

----, and ----. 1982. Reaction of wheat to common root rot: Linkage of a major gene, Crr, with the centromere to chromosome 5B. Can. J. Genet. Cytol. 24:19–25.

Latch, G.C.M. 1977. Incidence of barley yellow dwarf virus in ryegrass pastures in New Zealand. N.Z. J. Agric. Res. 20:87–89.

Latin, R.X., R.W. Harder, and M.V. Wiese. 1982. Incidence of Cephalosporium stripe as influenced by winter wheat management practices. Plant Dis. 66:229–230.

LeClerg, E.L., H.R. Adams, M.E. Bailey, C.E. Burkhead, H.T. Cook, C.D. Van Houweling, R.J. Anderson, J. Vermeer, and R.C. Wilson. 1965. Losses in agriculture. USDA Handb. 291. Government Printing Office, Washington, DC.

Ledingham, G.A. 1939. Studies on *Polymyxa graminis*, N. gen. N. N. sp., a plasmodiophoraceous root parasite. Can. J. Res. C17-38-51.

Ledingham, R.J., T.G. Atkinson, J.S. Horricks, J.T. Mills, L.J. Piening, and R.D. Tinline. 1972. Wheat losses due to common root rot in the Prairie provinces of Canada 1969–71. Can. Plant Dis. Surv. 53:113–122.

Lee, T.S., and G. Shaner. 1985a. Oligogenic inheritance of length of latent period in six slow leaf-rusting wheat cultivars. Phytopathology 75:636–643.

----, and ----. 1985b. Transgressive segregation of length of latent period in crosses between slow leaf-rusting wheat cultivars. Phytopathology 75:643–647.

Lewellen, R.T., E.L. Sharp, and E.R. Hehn. 1967. Major and minor genes in wheat for resistance to *Puccinia striiformis* and their responses to temperature changes. Can. J. Bot. 45:2155–2172.

Lindsten, K., B. Lindsten, M. Abdelmoeti, and N. Juntti. 1981. Purification and some properties of wheat dwarf virus. p. 27–34. R.T. Plumb (ed.) Proc. 3rd Conf. on Virus Diseases of gramineae in Europe. Rothamsted Exp. Stn., Harpenden, Herts., U.K.

Line, R.F. 1972. Chemical control of flag smut of wheat. Plant Dis. Rep. 56:636–640.

----. 1982. Chemical control of stripe rust and leaf rust of wheat in the Pacific Northwest. Phytopathology 72:338. (Abstr.)

----. 1983. Predicting stripe and leaf rust of wheat in northwestern United States. Phytopathology 73:768. (Abstr.)

Lipps, P.E., and Herr, L.J. 1982. Etiology of *Rhizoctonia cerealis* in sharp eyespot of wheat. Phytopathology 72:1574–1577.

Lister, R.M., and W.F. Rochow. 1979. Detection of barley yellow dwarf virus by enzyme-linked immunosorbent assay. Phytopathology 69:649–654.

Littlefield, L.J. 1981. Biology of the plant rusts. Iowa State Univ. Press, Ames.

----, and M.C. Heath. 1979. Ultrastructure of rust fungi. Academic Press, New York.

Loegering, W.Q. 1967. Stem rust of wheat. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:307–317.

Lowther, C.V. 1948. Low temperature as a factor in the germination of dwarf bunt chlamydospores. Phytopathology 38:309–310.

Luig, N.H. 1983. A survey of virulence genes in wheat stem rust, *Puccinia graminis* f. sp. *tritici*. Verlag Paul Parey, Berlin and Hamburg.

Luke, H.H., R.D. Barnett, and P.L. Pfahler. 1985. Influence of soil infestation, seed infection, and seed treatment on septoria nodorum blotch of wheat. Plant Dis. 69:74–76.

Luttrell, E.S. 1980. Host-parasite relationships and development of the ergot sclerotium in *Claviceps purpurea*. Can. J. Bot. 58:942–958.

Macer, R.C.F. 1961. The survival of *Cercosporella herpotrichoides* Fron in wheat straw. Ann. Appl. Biol. 49:165–172.

Maclean, D.J. 1982. Axenic culture of rust fungi. p. 37–120. *In* K. J. Scott and A.K. Chakravorty (ed.) The rust fungi. Academic Press, London.

Maloy, O.C., and R.J. Cook. 1981. Take-all in wheat: New developments for control. Wash. State Univ. Coop. Ext. Bull. EB0988.

Mantle, P.G. 1981. Effects of weed grasses on the ecology and distribution of ergot (*Claviceps purpurea*). p. 437–442. *In* J.M.Tresh (ed.) Pests, pathogens and vegetation. Pitman Publishing, Marshfield, MA.

----. and S. Shaw. 1976. Role of ascospore production by *Claviceps purpurea* in aetiology of ergot disease in male sterile wheat. Trans. Br. Mycol. Soc. 67:17–22.

----, ----, and D.A. Doling. 1977. Role of weed grasses in the etiology of ergot disease in wheat. Ann. Appl. Biol. 86:339–351.

Martens, J.W., W.L. Seaman, and T.G. Atkinson. 1984. Diseases of field crops in Canada. Canadian Phytopathological Society, Harrow, Ont.

Martin, J.M., D.E. Mathre, and R.H. Johnston. 1983a. Genetic variation for reaction to *Cephalosporium gramineum* in four crosses of winter wheat. Can. J. Plant Sci. 63:623–630.

Martin, R.A., and H.W. Johnston. 1982. Effects and control of Fusarium diseases of cereal grains in the Atlantic provinces. Can. J. Plant Pathol. 4:210–216.

Martin, T.J., W.W. Bockus, L.E. Browder, K.F. Finney, J.H. Hatchett, and D.L. Wetzel. 1983b. Registration of Arkan wheat. Crop Sci. 23:1221–1222.

----, T.L. Harvey, and R.W. Livers. 1976. Resistance to wheat streak mosaic virus and its vector, *Aceria tulipae*. Phytopathology 66:346–349.

----, ----, C.G. Bender, and D.L. Seifers. 1984. Control of wheat streak mosaic virus with vector resistance in wheat. Phytopathology 74:963–964.

Mathre, D.E., and R.H. Johnston. 1975. Cephalosporium stripe of winter wheat: Procedures for determining host response. Crop Sci. 15:591–594.

McBeath, J.H., and A.K. Vidaver. 1981. Bacterial mosaic disease on spring wheat and triticale in Alaska. Phytopathology 71:893–894. (Abstr.)

McIntosh, R.A. 1978. Breeding for resistance to powdery mildew in the temperate cereals. p. 237–257. *In* D.M. Spencer (ed.) The powdery mildews. Academic Press, London.

----. 1983. A catalogue of gene symbols for wheat (1983 edition). p. 1197–1254. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Fac. Agric., Kyoto University, Kyoto.

McKinney, H.H. 1937. Mosaic diseases of wheat and related cereals. USDA Bull. 442.

----. 1948. Wheats immune from soil-borne mosaic viruses in the field, susceptible when inoculated manually. Phytopathology 38:1003–13.

----. 1967. Virus diseases. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement, 1st ed. Agronomy, 13:355–374.

----, W.R. Paden, and B. Koehler. 1957. Studies on chemical control and overseasoning of, and natural inoculation with the soil-borne virus of wheat and oats. Plant Dis. Rep. 41:256–266.

McNeal, F.H., and E.L. Sharp. 1963. Effect of stripe rust on yield and test weight of white spring wheat varieties at Bozeman, Montana in 1962. Plant Dis. Rep. 47:763–765.

McVey, D.M., and K. Hamilton. 1985. Stem rust resistance gene from Triumph 64 identified in four other winter wheats. Plant Dis. 69:217–218.

Merkle, O.G., and E.L. Smith. 1983. Inheritance of resistance to soil borne mosaic in wheat. Crop Sci. 23:1075–1076.

Metcalfe, P.B., and J.F. Brown. 1969. Evaluation of nine fungicides in controlling flag smut of wheat. Plant Dis. Rep. 53:631–633.

Mitchell, J. 1946. The effects of phosphatic fertilizers on summerfallow wheat crops in certain areas of Saskatchewan. Sci. Agric. 26:566–577.

Modawi, R.S., E.G. Heyne, D. Brunetta, and W.G. Willis. 1982. Genetic studies of field reaction to wheat soilborne mosaic virus. Plant Dis. 66:1183–1184.

Moore, K.J., and R.J. Cook. 1984. Increased take-all of wheat with direct drilling in the Pacific Northwest. Phytopathology 74:1044–1049.

Morton, D.J., E. Tool, and I.K. Hagen. 1960. Procedure and effectiveness of the barley embryo test for loose smut used in North Dakota. Plant Dis. Rep. 44:802–803.

Morton, J.B., and D.E. Mathre. 1980. Identification of resistance to Cephalosporium stripe in winter wheat. Phytopathology 70:812–817.

Mountain, W.B. 1954. Studies of nematodes in relation to brown root rot in Ontario. Can. J. Bot. 32:737–759.

----. 1965. Pathogenesis by soil nematodes. p. 285–301. *In* K.F. Baker and W.C. Snyder (ed.) Ecology of soil-borne plant pathogens: Prelude to biological control. University of California Press, Berkeley.

Mower, R.L., W.C. Snyder, J.G. Hancock. 1975. Biological control of ergot by *Fusarium*. Phytopathology 65:5–10.

Mujake, N. 1938. Mendelian inheritance of resistance against the virus disease in wheat strains. Jpn. J. Genet. 14:239–242. (Plant Breed. Abstr. 1939, Vol. 8, p. 300.)

Mulligan, T.E. 1960. The transmission by mites, host-range and properties of ryegrass mosaic virus. Ann. Appl. Biol. 48:575–579.

Mundt, C.C., and J.A. Browning. 1985. Genetic diversity and cereal rust management. p. 523–556. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Murray, D.I.L. 1981. *Rhizoctonia solani* causing barley stunt disorder. Trans. Br. Mycol. Soc. 76:383–395.

Murray, T.D., and G.W. Bruehl. 1983. Role of the hypodermis and secondary cell wall thickening in basal stem internodes in resistance to strawbreaker foot rot in winter wheat. Phytopathology 73:261–268.

Nagarajan, S., and L.M. Joshi. 1985. Epidemiology in the Indian subcontinent. p. 309–400. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Nakagawa, M., Y. Soga, S. Watanabe, H. Gocho, and K. Nishio. 1959. Genetical studies on the wheat mosaic virus. II. Genes affecting the inheritance of susceptibility to strains of yellow mosaic virus in varietal crosses of wheat. Jpn. J. Breed. 9:118–120. (Plant Breed. Abstr. 1960, Vol. 30, p. 508.)

Nelson, L.R., D.D. Morey, and A.R. Brown. 1972. Severe leaf rust on wheat in Georgia. Plant Dis. Rep. 56:534–535.

----, ----, and ----. 1974. Wheat cultivar responses to severe glume blotch in Georgia. Plant Dis. Rep. 58:21–23.

Nelson, P.E., T.A. Toussoun, and R.J. Cook (ed.). 1981. *Fusarium* species: Diseases, biology, and taxonomy. Pennsylvania State University Press, University Park.

----, ----, and W.F.O. Marasas. 1983. *Fusarium* species: An illustrated manual for identification. Pennsylvania State University Press, University Park.

Nema, K.G., G.S. Dave, and H.K. Khosla. 1971. A new glume blotch of wheat. Plant Dis. Rep. 55:95.

Niblett, C.L., M.A. Newman, R.W. Livers, and J.R. Young. 1976. Strains of wheat streak mosaic virus. Annu. Wheat Newsl. 22:85–86.

Nielsen, J. 1972. Isolation and culture of monokaryotic haplonts of *Ustilago tritici*, observations on their physiology, and the taxonomic relationship between *U. tritici* and *U. nuda*. Can. J. Bot. 50:1775–1781.

----. 1978. Host range of the smut species *Ustilago nuda* and *Ustilago tritici* in the tribe Triticeae. Can. J. Bot. 56:901–915.

Nykaza, S.M., E.G. Heyne, and C.L. Niblett. 1979. Effects of wheat soilborne mosaic on several plant characters of winter wheat. Plant Dis. Rep. 63:594–598.

Ohm, H.W., and G.E. Shaner. 1976. Three components of slow leaf-rusting at different growth stages in wheat. Phytopathology 66:1356–1360.

Orlob, G.B. 1966. Feeding and transmission characteristics of *Aceria tulipae* Keifer as vector of wheat streak mosaic virus. Phytopathol. Z. 55:218–238.

Otta, J.D. 1974. *Pseudomonas syringae* incites a leaf necrosis on spring and winter wheats in South Dakota. Plant Dis. Rep. 58:1061–1064.

----. 1977. Occurrence and characteristics of isolates of *Pseudomonas syringae* on winter wheat. Phytopathology 67:22–26.

Paliwal, Y.C. 1978. Purification and some properties of barley yellow dwarf virus. Phytopathol. Z. 92:240–246.

----, and C.J. Andrews. 1979. Effects of barley yellow dwarf and wheat spindle streak mosaic viruses on cold hardiness of cereals. Can. J. Plant Pathol. 1:71–75.

Palm, E.W. 1982. Wheat streak mosaic of wheat in Missouri—1981. Phytopathology 72:961.

Palmer, L.T., and M.K. Brakke. 1975. Yield reduction in winter wheat infected with soilborne wheat mosaic virus. Plant Dis. Rep. 59:469–471.

Panayotou, P.C. 1977. Effect of barley yellow dwarf on several varieties of maize. Plant Dis. Rep. 61:815–819.

Parlevliet, J.E. 1981. Disease resistance in plants and its consequences for plant breeding. p. 309–364. *In* K.J. Frey (ed.) Plant breeding II. Iowa State University Press, Ames.

----. 1985. Resistance of the non race-specific type. p. 497–521. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Parmeter, J.R., Jr. 1970. *Rhizoctonia solani*, biology and pathology. University of California Press, Berkeley.

Patterson, F.L., G.E. Shaner, D.M. Huber, H.W. Ohm, R.E. Finney, R.L. Gallun, and J.J. Roberts. 1979. Registration of Sullivan wheat. Crop Sci. 19:297.

----, G.E. Shaner, H.W. Ohm, C.M. Brown, and H. Jedlinski. 1983. Rosette wheat germplasm. Crop Sci. 23:1022–1023.

Pearce, R.B., R.N. Strange, and H. Smith. 1976. Glycinebetaine and choline in wheat: Distribution and relation to infection by *Fusarium graminearum*. Phytochemistry 15:953–954.

Perry, V.G. 1953. Return of nematodes following fumigation of Florida soils. Proc. Florida State Hortic. Soc. 66:112–114.

----, and H.L. Rhoades. 1982. The Trichodorid nematodes. p. 193–196. *In* Nematology in the southern region of the United States. Southern Coop. Serv. Bull. 276.

Pfannenstiel, M.A., and C.L. Niblett. 1978. The nature of the resistance of Agrotricums to wheat streak mosaic virus. Phytopathology 68:1204–1209.

Pitt, D. 1964. Studies on sharp eyespot disease of cereals. Ann. Appl. Biol. 54:77–89.

Platford, R.G., and C.C. Bernier. 1970. Resistance to *Claviceps purpurea* in spring and durum wheats. Nature (London) 226:770.

----, and ----. 1976. Reaction of cultivated cereals to *Claviceps purpurea*. Can. J. Plant Sci. 56:51–58.

----, ----, and L.E. Evans. 1977. Chromosome location of genes conditioning resistance to *Claviceps purpurea* in spring and durum wheat. Can. J. Genet. Cytol. 19:679–682.

Plumb, R.T. 1983. Barley yellow dwarf virus—A global problem. p. 185–198. *In* R.T. Plumb. and J.M. Thresh (ed.) Plant Virus Epidemiology. Blackwell Scientific Publications, Oxford.

----. 1984. Chemical and cultural control of barley yellow dwarf. p. 52–57. *In* P. Burnett (ed.) Barley Yellow Dwarf: Proceedings of the Workshop. 6–8 December 1983. CIMMYT, Mexico.

----, and E.A. Lennon. 1981. Agropyron mosaic virus in wheat. p. 55–60. *In* R.T. Plumb (ed.) Proc. 3rd Conf. Virus Diseases of Gramineae in Europe. Rothamsted Agric. Exp. Stn., Herpenden, Herts, U.K.

Poinso, B., B. Alliot, and P.A. Signoret. 1981. A mite-transmitted virus occurring on gramineae in southern France. p. 35–44. *In* R.T. Plumb (ed.) Proc. of 3rd Conference on Virus Diseases of Gramineae in Europe. Rothamsted Agric. Exp. Stn., Harpenden, Herts., U.K.

Potter, L.R. 1980. The effects of barley yellow dwarf virus and powdery mildew in oats and barley with single and dual infection. Ann. Appl. Biol. 94:11–17.

----. 1982. Interaction between barley yellow dwarf virus and rust in wheat, barley and oats, and the effects on grain yield and quality. Ann. Appl. Biol. 100:321–329.

Powelson, R.L. 1982. Fungicide evaluation for control of wheat Cercosporella foot rot, 1981. Fung. Nema Tests 37:121.

----, and T.L. Jackson. 1978. Suppression of take-all (*Gaeumannomyces graminis*) root rot of wheat with fall applied chloride fertilizers. p. 175–182. *In* Proc. 29th Annu. Northwest Fertilizer Conf., Beaverton, Oregon, 11–13 July.

Prabhu, A.S., and R. Prasada. 1966. Pathological and epidemiological studies on leaf blight of wheat caused by *Alternaria triticina*. Ind. Phytopathol. 19:95–112.

Prevost, B. 1807. Memoir on the immediate cause of bunt or smut of wheat, and of several other diseases of plants, and on preventives of rust. Transl. from French by G.W. Keitt. Phytopathol. classics 6. American Phytopathological Society. Madison, WI (1939).

Purdy, L.H. 1957. Differential response of dwarf bunt to seed and soil surface treatment with hexachlorobenzene. Plant Dis. Rep. 41:916–918.

----. 1965. Flag smut of wheat. Bot. Rev. 31:565–606.

----, J.A. Hoffmann, J.P. Meiners, and V.R. Stewart. 1963. Time of year of infection of winter wheat by the dwarf bunt fungus. Phytopathology 53:1419–1421.

----, E.L. Kendrick, J.A. Hoffmann, and C.S. Holton. 1963. Dwarf bunt of wheat. Annu. Rev. Microbiol. 17:199–221.

Purss, G.S. 1971. Pathogenic specialization in *Fusarium graminearum*. Aust. J. Agric. Res. 22:553–561.

Qualset, C.O., P.E. McGuire, H.E. Vogt, and M.A. Topcu. 1977. Ethiopia as a source of resistance to the barley yellow dwarf virus in tetraploid wheat. Crop Sci. 17:527–529.

----, J.C. Williams, M.A. Topcu, and H.E. Vogt. 1973. The barley yellow dwarf virus in wheat: Importance sources of resistance, and heritability. p. 465–470. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Quisenberry, K.S., and L.P. Reitz (ed.) 1967. Wheat and wheat improvement. 1st ed. Agronomy 13.

Rahman, F., J.G. Ross, and W.S. Gardner. 1974. Tolerance to wheat streak mosaic virus in spring and winter wheat cultivars. Crop Sci. 14:178–180.

Rao, A.S. 1968. Biology of *Polymyxa graminis* in relation to soil-borne wheat mosaic virus. Phytopathology 58:1516–1521.

----, and M.K. Brakke. 1969. Relation of soil-borne wheat mosaic virus and its fungal vector *Polymyxa graminis*. Phytopathology 59:581–587.

----, and ----. 1970. Dark treatment of wheat inoculated with soil-borne wheat mosaic and barley stripe mosaic viruses. Phytopathology 60:714–716.

Rapilly, F. 1977. Recherche des facteurs de résistance horizontale à la septoriose du blé (*Septoria nodorum* Berk.): Résultats obtenus par la simulation (1). Ann. Phytopathol. 9:1–19.

Raymond, P.J., and W.W. Bockus. 1984. Effect of seeding date of winter wheat on incidence, severity, and yield loss caused by Cephalosporium stripe in Kansas. Plant Dis. 68:665–667.

Rees, R.G., and G.J. Platz. 1979. The occurrence and control of yellow spot of wheat in north-eastern Australia. Aust. J. Exp. Agric. Anim. Husb. 19:369–372.

----, and ----. 1980. The epidemiology of yellow spot of wheat in southern Queensland. Aust. J. Agric. Res. 31:259–267.

----, and ----. 1983. Effects of yellow spot on wheat: Comparisons of epidemics at different stages of crop development. Aust. J. Agric. Res. 34:39–46.

Reitz, L.P., and S.C. Salmon. 1959. Hard red winter wheat improvement in the plains. USDA Tech. Bull. 1192. U. S. Printing Office. Washington, D.C.

Richardson, M.J., and W.J. Rennie. 1970. An estimate of the loss of yield caused by *Cephalosporium gramineum* in wheat. Plant Pathol. 19:138–140.

----, and F.J. Zillinsky. 1972. A leaf blight caused by *Fusarium nivale*. Plant Dis. Rep. 56:803–804.

Rillo, A.O., R.M. Caldwell, and D.V. Glover. 1970. Cytogenetics of resistance to wheat leaf blotch (*Septoria tritici*) in backcross derivatives of an Agrotrichum line. Crop Sci. 10:223–227.

Robbelen, G., and E.L. Sharp. 1978. Mode of inheritance, interaction and application of genes conditioning resistance to yellow rust. Verlag Paul Parey, Berlin and Hamburg.

Roberts, J.J., and R.M. Caldwell. 1970. General resistance (slow mildewing) to *Erysiphe graminis* f. sp. *tritici* in Knox wheat. Phytopathology 60:1310. (Abstr.)

----, L.T. Hendricks, and F.L. Patterson. 1984. Tolerance to leaf rust in susceptible wheat cultivars. Phytopathology 74:349–351.

Rochow, W.F. 1960. Specialization among greenbugs in the transmission of barley yellow dwarf virus. Phytopathology 50:881–884.

----. 1961. The barley yellow dwarf virus disease of small grains. Adv. Agron. 13:217–248.

----. 1970a. Barley yellow dwarf virus: Phenotypic mixing and vector specificity. Science 167:875–878.

----. 1970b. Barley yellow dwarf virus. C.M.I./A.A.B. description of plant viruses no. 32. Commonwealth Mycological Institute, Surrey, U.K.

----. 1979. Field variants of barley yellow dwarf virus: Detection and fluctuation during twenty years. Phytopathology 69:655–660.

----. 1982. Identification of barley yellow dwarf viruses: Comparison of biological and serological methods. Plant Disease 66:381–384.

----, and M.K. Brakke. 1964. Purification of barley yellow dwarf virus. Virology. 24:310–322.

----, and J.E. Duffus. 1981. Luteoviruses and yellows diseases. *In* E. Kurstak (ed.) Handbook of plant virus diseases and comparative diagnosis. Elsevier North Holland Biomedical Press, Amsterdam.

----, and C.C. Gill. 1978. Dependent virus transmission by *Rhopalosiphum padi* from mixed infections of various isolates of barley yellow dwarf virus. Phytopathology 68:451–456.

Roelfs, A.P. 1978. Estimated losses caused by rust in small grain cereals in the United States—1918–76. USDA Misc. Pub. 1363. U. S. Printing Office, Washington, D.C.

----. 1982. Effects of barberry eradication on stem rust in the United States. Plant Dis. 66:177–181.

----. 1985a. Wheat and rye stem rust. p. 3–37. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

----. 1985b. Epidemiology in North America. p. 401–432. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

----. 1986. Development and impact of regional cereal rust epidemics. p. 129–150. *In* K.J. Leonard and W.E. Fry (ed.) Plant disease epidemiology: Population dynamics and management, Vol. 1. Macmillan, New York.

----, and D.V. McVey. 1979. Low infection types produced by *Puccinia graminis* f. sp. *tritici* and wheat lines with designated genes for resistance. Phytopathology 69:722–730.

Rohde, R.A., and W.R. Jenkins. 1957a. Effect of temperature on the life cycle of the stubby-root nematodes. Phytopathology 47:29. (Abstr.)

----, and ----. 1957b. Host range of a species of *Trichodorus* and its host–parasite relationships on tomatoes. Phytopathology 47:295–298.

Rosielle, A.A. 1972. Sources of resistance in wheat to speckled leaf blotch caused by *Septoria tritici*. Euphytica 21:152–161.

----, and Brown, A.G.P. 1979. Inheritance, heritability and breeding behaviour of three sources of resistance to *Septoria tritici* in wheat. Euphytica 28:385–392.

Rowe, R.C., and R.L. Powelson. 1973a. Epidemiology of Cercosporella foot rot of wheat: disease spread. Phytopathology 63:984–988.

----, and ----. 1973b. Epidemiology of Cercosporella foot rot of wheat: Spore production. Phytopathology 63:981–984.

Rowell, J.B. 1981. Control of stem rust of spring wheat by Triadimefon and Fenapanil. Plant Dis. 65:235–236.

----. 1982. Control of wheat stem rust by low receptivity to infection conditioned by a single dominant gene. Phytopathology 72:297–299.

----. 1985. Evaluation of chemicals for rust control. p. 557–585. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Russell, C.C. 1962. The embryology and parasitic habit of *Trichodorus christiei* Allen with observations of predators. M.S. thesis. University of Florida, Gainesville.

----, and V.G. Perry. 1966. Parasitic habit of *Trichodorus christiei* on wheat. Phytopathology 56:357–358.

Russell, R.C., and W. Popp. 1951. The embryo test as a method of forecasting loose-smut infection in barley. Sci. Agric. 31:559–565.

Saari, E.E., and J.M. Prescott. 1985. World distribution in relation to economic losses. p. 259–298. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

----, and R.D. Wilcoxson. 1974. Plant disease situations of high-yielding dwarf wheats in Asia and Africa. Ann. Rev. Phytopathol. 12:49–68.

Saito, Y., K. Takanashi, Y. Iwata, and H. Okamoto. 1964. Studies on the soil-borne virus diseases of wheat and barley. III. Influence of chemicals on the infected soils and the viruses. Bull. Natl. Inst. Agric. Sci. Ser. C 17:41–59.

Sallans, B.J. 1965. Root rots of cereals. III. Bot. Rev. 32:505–536.

Samborski, D.J. 1985. Leaf rust of wheat. p. 39–59. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Samuel, G., and S.D. Garrett. 1932. *Rhizoctonia solani* on cereals in south Australia. Phytopathology 22:827–836.

Sanderson, F.R., and Hampton, J.G. 1978. Role of the perfect stages in the epidemiology of the common *Septoria* diseases of wheat. N.Z.J. Agric. Res. 21:277–281.

Savile, D.B.O. 1984. Taxonomy of the cereal rust fungi. p. 79–112. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

----, and Z. Urban. 1982. Evolution and ecology of *Puccinia graminis*. Preslia 54:97–104.

Schaad, N.W., and Forster, R.L. 1985. A semiselective medium for isolating *Xanthomonas campestris* pv. *translucens* from wheat seeds. Phytopathology 75:260–263.

Schafer, J.F. 1971. Tolerance to plant disease. Annu. Rev. Phytopathol. 9:235–252.

----. 1974. Host plant resistance to plant pathogens and insects: History, current status, and future outlook. p. 238–247. *In* F.G. Maxwell and F.A. Harris (ed.) Proc. Summer Inst. Biol. Control Plant Insects and Dis. Univ. of Mississippi Press, Jackson.

----, R.M. Caldwell, F.L. Patterson, L.E. Compton, R.L. Gallun, and J.J. Roberts. 1968. Arthur soft red winter wheat, a breakthrough to a new yield level. Purdue Univ. Agric. Exp. Stn. Prog. Rep. 335.

----, and A.P. Roelfs. 1985. Estimated relation between numbers of urediniospores of *Puccinia graminis* f. sp. *tritici* and rates of occurrence of virulence. Phytopathology 75:749–750.

----, ----, and W.R. Bushnell. 1984. Contributions of early scientists to knowledge of cereal rusts. p. 3–38. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

Scharen, A.L. 1964. Environmental influences on development of glume blotch in wheat. Phytopathology 54:300–303.

----, J.W. Bergman, and E.E. Burns. 1976. Leaf diseases of winter wheat in Montana and losses from them in 1975. Plant Dis. Rep. 60:686–690.

----, and J.M. Krupinsky. 1971. *Ascochyta tritici* on wheat. Phytopathology 61:675–680.

Scott, K.J. 1972. Obligate parasitism by phytopathogenic fungi. Biol. Rev. 47:537–572.

Scott, P.R., P.W. Benedikz, and C.J. Cox. 1982. A genetic study of the relationship between height, time of ear emergence and resistance to *Septoria nodorum* in wheat. Plant Pathol. 31:45–60.

Sellam, M.A., and R.D. Wilcoxson. 1976. Bacterial leaf blight of wheat in Minnesota. Plant Dis. Rep. 60:242–245.

Shaalan, M.I., E.G. Heyne, and W.H. Sill, Jr. 1966. Breeding wheat for resistance to soilborne wheat mosaic virus, wheat streak mosaic virus, leaf rust, stem rust and bunt. Phytopathology 56:664–668.

Shaner, G. 1972. Performance of two fungicides against wheat powdery mildew in the field. Plant Dis. Rep. 56:358–362.

----. 1980. Probits for analyzing latent period data in studies of slow rusting resistance. Phytopathology 70:1179–1182.

----. 1981. Effect of environment on fungal leaf blights of small grains. Ann. Rev. Phytopathol. 19:273–296.

----, and R.E. Finney. 1977. The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. Phytopathology 67:1051–1056.

----, ----, and F.L. Patterson. 1975. Expression and effectiveness of resistance in wheat to Septoria leaf blotch. Phytopathology 65:761–766.

----, and F.D. Hess. 1978. Equations for integrating components of slow leaf-rusting resistance in wheat. Phytopathology 68:1464–1469.

Sharp, E.L., C.R. Perry, A.L. Scharen, G.O. Boatwright, D.C. Sands, L.F. Lautenschlager, C.M. Yahyaoui, and F.W. Ravet. 1985. Monitoring cereal rust development with a spectral radiometer. Phytopathology 75:936–939.

Shaw, B.L., and P.G. Mantle. 1980. Host infection by *Claviceps purpurea*. Trans. Br. Mycol. Soc. 75:77–90.

Shearer, B.L., and R.D. Wilcoxson. 1980. Sporulation of *Septoria* species on wheat and barley in Minnesota. Minn. Agric. Exp. Stn. Tech. Bull. 323.

Shipton, P.J. 1975. Take-all decline during cereal monoculture. p. 137–144. *In* G.W. Bruehl (ed.) Biology and control of soilborne plant pathogens. American Phytopathological Society, St. Paul.

----, R.J. Cook, and J.W. Sitton. 1973. Occurrence and transfer of a biological factor in soil that suppresses take-all of wheat in eastern Washington. Phytopathology 63:511–517.

Shipton, W.A., W.R.J. Boyd, A.A. Rosielle, and B.L. Shearer. 1971. The common Septoria diseases of wheat. Bot. Rev. 37:231–262.

----, and S.C. Chambers. 1966. The internal microflora of wheat grains in western Australia. Aust. J. Exp. Agric. Anim. Husb. 6:432–436.

Shirako, Y., and M.K. Brakke. 1984a. Two purified RNAs of soil-borne wheat mosaic virus are needed for infection. J. Gen. Virol. 65:119–127.

----, and ----. 1984b. Spontaneous deletion mutation of soil- borne wheat mosaic virus RNA II. J. Gen. Virol. 65:855–858.

Signoret, P.A., and B. Alliot. 1981. A new virus disease of maize in France. p. 1–8. *In* R.T. Plumb (ed.) Proc. 3rd Conf. Virus Diseases of Gramineae in Europe. Rothamsted Agric. Exp. Stn., Harpenden, Herts., U.K.

----, ----, and B. Poinso. 1977. Présence en France du Wheat Spindle Streak Mosaic Virus. Ann. Phytopathol. 9:377–379.

Sill, W.H. Jr., and P.C. Agusiobo. 1955. Host range studies of the wheat streak mosaic virus. Plant Dis. Rep. 39:633–642.

Simmonds, P.W. 1946. Detection of the loose smut fungi in embryos of barley and wheat. Sci. Agric. 26:51–58.

Simonovich, I.D., L.T. Pastushenko, and I.B. Koroleva. 1977. [The diagnosis of basal bacteriosis of wheat]. Zasch. Rast. 7:34–35. (In Russian.) Abstr. in Rev. Plant Pathol. 57 #2497, 1979.

Simons, M.D. 1969. Heritability of crown rust tolerance in oats. Phytopathology 59:1329–1333.

Sitton, J.W., and R.J. Cook. 1981. Comparative morphology and survival of chlamydospores of *Fusarium roseum* 'Culmorum' and 'Graminearum.' Phytopathology 71:85–90.

Slope, D.B., and J. Cox. 1964. Continuous wheat growing and the decline of take-all. Rep. Rothamsted Exp. Stn. 1963. Pt. 1, 108.

Slykhuis, J.T. 1953. Wheat streak mosaic in Alberta and factors related to its spread. Can. J. Agric. Sci. 33:195–197.

----. 1955. *Aceria tulipae* Keifer (Acarina: Eriophyidae) in relation to the spread of wheat streak mosaic. Phytopathology 45:116–128.

----. 1967. Virus diseases of cereals. Rev. Appl. Mycol. 46:401–429.

----. 1970. Factors determining the development of wheat spindle streak mosaic caused by a soil-borne virus in Ontario. Phytopathology 60:319–331.

----. 1973. Agropyron mosaic virus. C.M.I./A.A.B. descriptions of plant viruses no. 118. Commonwealth Mycological Institute, Surrey, U.K.

----. 1974. Differentiation of transmission and incubation temperatures for wheat spindle streak mosaic virus. Phytopathology 64:554–557.

----. 1976. Wheat Spindle Streak Mosaic Virus. C.M.I./A.A.B. descriptions of plant viruses no. 167. Commonwealth Mycological Institute, Surrey, U.K.

----, J.E. Andrews, and U.J. Pittman. 1957. Relation of date of seeding winter wheat in southern Alberta to losses from wheat streak mosaic, root rot, and rust. Can. J. Plant Sci. 37:113–127.

----, and D.J.S. Barr. 1978. Confirmation of *Polymyxa graminis* as a vector of wheat spindle streak mosaic virus. Phytopathology 68:639–643.

----, and Z. Polak. 1969. Verification of wheat spindle streak virus as a cause of mosaic of wheat in Ontario. Can. Plant Dis. Surv. 49:108–111.

----, and ----. 1971. Factors affecting manual transmission, purification, and particle lengths of wheat spindle streak mosaic virus. Phytopathology 61:569–574.

Smiley, R.W., and R.J. Cook. 1973. Relationship between take-all of wheat and rhizosphere pH in soils fertilized with ammonium vs. nitrate nitrogen. Phytopathology 63:882–890.

Smith, H.C. 1962. Is barley yellow dwarf virus a predisposing factor in common root rot disease in Canada? Can. Plant Dis. Surv. 42:143–148.

----. 1963a. Interaction between isolates of barley yellow dwarf virus. N.Z. J. Agric. Res. 6:343–353.

----. 1963b. Control of barley yellow dwarf virus in cereals. N.Z. J. Agric. Res. 6:229–44.

----, and G.M. Wright. 1964. Barley yellow dwarf virus on wheat in New Zealand. N.Z. Wheat Rev. 9:60–79.

Smith, N.A., R.P. Scheffer, and A.H. Ellingboe. 1966. Cephalosporium stripe of wheat prevalent in Michigan. Plant Dis. Rep. 50:190–191.

Speakman, J.B. 1982. A simple, reliable method of producing perithecia of *Gaemannomyces graminis* var. *tritici* and its application to isolates of *Phialophora* spp. Trans. Br. Mycol. Soc. 79:350–353.

Sprague, R. 1950. Diseases of cereals and grasses in North America. Ronald Press, New York.

Stack, R.W. 1982. Root and crown rots of small grains. Coop. Ext. Serv. Circ. PP-785. North Dakota State University, Fargo.

Stakman, E.C. 1923. Barberry eradication prevents black rust in Western Europe. USDA Circ. 269. U.S. Printing Office, Washington, D.C.

----, and J.G. Harrar. 1957. Principles of plant pathology. Ronald Press, New York.

----, and R.J. Piemeisel. 1917. Biologic forms of *Puccinia graminis* on cereals and grasses. J. Agric. Res. 10:429–495.

Staples, Robert, and W.B. Allington. 1956. Streak mosaic of wheat in Nebraska and its control. Nebraska Agric. Exp. Stn. Res. Bull. 178.

Staples, R.C., and V. Macko. 1984. Germination of urediospores and differentiation of infection structures. p. 255–289. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

Statler, G.D., and L.C. Darlington. 1972. Resistance of hard red spring wheat and durum wheat to seedling blight and crown rot. Plant Dis. Rep. 56:788–791.

----, R.L. Kiesling, and R.H. Busch, 1975. Inheritance of black point resistance in durum wheat. Phytopathology 65:627–629.

Stern, R.E., and J.P. Jones. 1978. Sharp eyespot of wheat in Arkansas caused by *Rhizoctonia solani*. Plant Dis. Rep. 62:56–60.

Stewart, V.R., and E.R. Hehn. 1967. Effect of stripe rust on yield and its components of six winter wheat varieties. Plant Dis. Rep. 51:702–705.

Strange, R.N., A. Deramo, and H. Smith. 1978. Virulence enhancement of *Fusarium graminearum* by choline and betaine and of *Botrytis cinerea* by other constituents of wheat germ. Trans. Br. Mycol. Soc. 70:201–207.

----, J.R. Majer, and H. Smith. 1974. The isolation and identification of choline and betaine as the two major components in anthers and wheat germ that stimulate *Fusarium graminearum* in vitro. Phys. Plant Pathol. 4:277–290.

----, and H. Smith. 1971. A fungal stimulant in anthers which predisposes wheat to attack by *Fusarium graminearum*. Phys. Plant Pathol. 1:141–150.

----, and ----. 1978. Specificity of choline and betaine as stimulants of *Fusarium graminearum*. Trans. Br. Mycol. Soc. 70:187–192.

Stubbs, R.W. 1985. Stripe rust. p. 61–101. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Sung, J.M., and R.J. Cook. 1981. Effect of water potential on reproduction and spore germination by *Fusarium roseum* 'Graminearum', 'Culmorum', and 'Avenaceum'. Phytopathology 71:499–504.

Suryanarayana, D., and M.C. Mukhopadhaya. 1971. Earcockle and 'tundu' disease of wheat. Ind. J. Agric. Sci. 41:407–413.

Sutton, J.C. 1982. Epidemiology of wheat head blight and maize ear rot caused by *Fusarium graminearum*. Can. J. Plant Pathol. 4:195–209.

Sutton, M.D. 1966. Bacteriophages of *Pseudomonas atrofaciens* in cereal seeds. Phytopathology 56:727–730.

Targioni Tozzetti, G. 1767. True nature, causes and sad effects of the rust, the bunt, the smut, and other maladies of wheat and of oats in the field. Transl. from Italian by L.R. Tehon. Phytopathol. classics no. 9. American Phytopathological Society, St. Paul (1952).

Taylor, R.G., R.L. Jackson, R.L. Powelson, and N.W. Christensen. 1983. Chloride, nitrogen form, lime, and plant date effects on take-all root rot of winter wheat. Plant Dis. 67:1116–1120.

Thames, W.H. 1982. The genus *Pratylenchus*. p. 108–126. *In* Nematology in the southern region of the United States. Southern Coop. Ser. Bull. 276.

Tillet, M. 1755. Dissertation on the cause of the corruption and smutting of the kernels of wheat in the head. Transl. from French by H.B. Humphrey. Phytopathol. classics 5. American Phytopathological Society, Ithaca, NY (1937).

Todd, T.C. 1980. Disease interaction of *Pratylenchus neglectus* and *Fusarium* spp. on winter wheat with a comparison of nematode root incubation techniques. M.S. thesis. Oklahoma State University, Stillwater.

Tola, J.E., and W.E. Kronstad. 1984. The genetics of resistance to barley yellow dwarf virus in wheat. p. 83–91. *In* P. Burnett (ed.) Barley Yellow Dwarf: Proceedings of the Workshop. 6–8 December 1983. CIMMYT, Mexico.

Tosic, M. 1973. Transmission of wheat streak mosaic virus to different host plants by *Aceria tosichella*. Plant Prot. (Belgrade) 126:317–321.

Trelease, S.F., and H.M. Trelease. 1929. Susceptibility of wheat to mildew as influenced by carbohydrate supply. Bull. Torrey Bot. Club 56:65–92.

Trione, E.J. 1982. Dwarf bunt of wheat and its importance in international wheat trade. Plant Dis. 66:1083–1088.

Troutman, J.L. and J.C. Matejka. 1972. Downy mildew of small grains and sorghum in Arizona. Plant Dis. Rep. 56:773–774.

Tsuchizaki, T., H. Hibino, and Y. Saito. 1973. Comparison of soil-borne wheat mosaic virus isolates from Japan and the United States. Phytopathology 63:634–639.

----, ----, and ----. 1975. The biological functions of short and long particles of soil-borne wheat mosaic virus. Phytopathology 65:523–532.

Tyler, D.J., and L.E. Dickens. 1957. Cephalosporium leaf stripe disease of winter wheat. Plant Dis. Rep. 41:384.

Usugi, T., and Y. Saito. 1976. Purification and serological properties of barley yellow mosaic and wheat yellow mosaic virus. Ann. Phytopathol. Soc. Jpn. 42:12–20.

----, and ----. 1979. Relationship between wheat yellow mosaic virus and wheat spindle streak mosaic virus. Ann. Phytopathol. Soc. Jpn. 45:397–400.

Vanderplank, J.E. 1963. Plant diseases: Epidemics and control. Academic Press, New York.

Van Rensburg, S.J., and B. Altenkirk. 1974. *Claviceps purpurea*–ergotism. p. 69–96. *In* I.F.H. Purchase (ed.) Mycotoxins. Elsevier Scientific Publ. Co., New York.

Vanterpool, T.C. 1952. The phenomenal decline of browning root rot (*Pythium* spp.) on the Canadian prairies. Sci. Agric. (Ottawa) 32:443–452.

Varughese, J., and E. Griffiths. 1983. Effect of barley yellow dwarf virus on susceptibility of barley cultivars to net blotch (*Pyrenophora teres*) and leaf blotch (*Rhynchosporium secalis*). Plant Pathol. 32:435–440.

Vidaver, A.K. 1982. The plant pathogenic corynebacteria. Annu. Rev. Microbiol. 36:495–517.

von Schmeling, B., and M. Kulka. 1968. The systemic fungicide 2,3-dihydro-5-carboxanilido-6-methyl-1,4-oxathiin. p. 1–2. *In* J.G. Moseman (ed.) Fungicidal control of smut diseases of cereals. USDA–ARS CR 42–68.

Von Wechmar, M.B., and E.P. Rybicki. 1985. Brome mosaic virus infection mimics barley yellow dwarf disease symptoms in small grains. Phytopath. Zeit. 114:332–337.

Walker, J. 1975. Take-all diseases of Gramineae: A review of recent work. Rev. Plant Pathol. 54:113–144.

Wallin, J.R., D. Peters, and L.C. Johnson. 1967. Low-level jet winds, early cereal aphid and barley yellow dwarf virus detection in Iowa. Plant Dis. Rep. 51:527–530.

Watkins, J.E., M.G. Boosalis, and E.D. Kerr. 1980. Root and crown rot of winter wheat. Nebraska Coop. Ext. Serv. Bull. G 80–483.

----, G.N. Odvody, M.G. Boosalis, and J.E. Partridge. 1978. An epidemic of tan spot in Nebraska. Plant Dis. Rep. 62:132–134.

Watson, I.A., and D. Singh. 1952. The future of rust resistant wheat in Australia. J. Aust. Inst. Agric. Sci. 18:190–197.

Weller, D.M., and R.J. Cook. 1983. Suppression of take-all of wheat by seed treatments with fluorescent pseudomonads. Phytopathology 73:463–469.

Wells, D.G., R.S. Kota, H.S. Sandhu, W.S. Gardner, and K.F. Finney. 1982. Registration of one disomic substitution line and five translocation lines of winter wheat germplasm resistant to wheat streak mosaic virus. Crop Sci. 22:1277–1278.

Weste, G., and L.B. Thrower. 1963. Production of perithecia and microconidia in culture by *Ophiobolus graminis*. Phytopathology 53:354.

White, J.L., and M.K. Brakke. 1983. Protein changes in wheat infected with wheat streak mosaic virus and in barley infected with barley stripe mosaic virus. Physiol. Plant Pathol. 22:87–100.

Wiese, M.V. 1987. Compendium of wheat diseases, 2nd edition. American Phytopathological Society, St. Paul, MN.

----, and A.V. Ravenscroft. 1975. *Cephalosporium gramineaum* populations in soil under winter wheat cultivation. Phytopathology 65:1129–1133.

----, ----, and V. Everson. 1974. Incidence of wheat spindle streak mosaic among ten wheat cultivars and its effect on yield. Plant Dis. Rep. 58:522–525.

Wilcoxson, R.D. 1981. Genetics of slow rusting in cereals. Phytopathology 71:989–993.

Wilhelm, S. 1965. *Pythium ultimum* and the soil fumigation response. Phytopathology 55:1016–1020.

Wilkie, J.P. 1973. Basal glume rot of wheat in New Zealand. N.Z. J. Agric. Res. 16:155–160.

Williams, A.S., T.P. Pirone, J.T. Slykhuis, and C.R. Tutt. 1975. Wheat spindle streak mosaic virus in Kentucky. Plant Dis. Rep. 59:888–889.

Williams, P.G. 1984. Obligate parasitism and axenic culture. p. 399–430. *In* W.R. Bushnell and A.P. Roelfs (ed.) The cereal rusts, Vol. 1. Academic Press, Orlando, FL.

Willis, W.G., and O.D. Shively. 1974. Cephalosporium stripe of winter wheat and barley in Kansas. Plant Dis. Rep. 58:566–567.

Wolf, J.C., J.R. Lieberman, and C.J. Mirocha. 1972. Inhibition of F-2 (zearalenone) biosynthesis and perithecium production in *Fusarium roseum* 'Graminearum'. Phytopathology 62:937–939.

----, and C.J. Mirocha. 1973. Regulation of sexual reproduction in *Gibberella zeae* (*Fusarium roseum* 'Graminearum') by F-2 (zearalenone). Can. J. Microbiol. 19:725–734.

Wood, G., and J.R. Coley-Smith. 1982. Epidemiology of ergot disease (*Claviceps purpurea*) in open-flowering male-sterile cereals. Ann. Appl. Biol. 100:73–82.

Yarwood, C.E. 1957. Powdery mildews. Bot. Rev. 23:235–301.

----. 1973. Pyrenomycetes: Erysiphales. p. 71–86. *In* G.C. Ainsworth et al. (ed.) The fungi: An advanced treatise, Vol. 4A. Academic Press, New York.

----. 1978. History and taxonomy of powdery mildews. p. 1–37. *In* D.M. Spencer (ed.) The powdery mildews. Academic Press, London.

Young, H.C., Jr., and F.B. Struble. 1966. Effect of temperature on the development of *Trichodorus christiei* on wheat. Phytopathology 56:907 (Abstr.)

Yount, D.J., and T.W. Carroll. 1983. Barley yellow dwarf luteovirus in Montana cereals. Plant Dis. 67:1217–1222.

Zadoks, J.C., and J.J. Bouwman. 1985. Epidemiology of cereal rusts in Europe. p. 327–367. *In* A.P. Roelfs and W.R. Bushnell (ed.) The cereal rusts, Vol. 2. Academic Press, Orlando, FL.

Zeller, F.J. 1973. IB/IR wheat–rye chromosome substitutions and translocations. p. 209–221. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, Mo. 6–11 August 1973. University of Missouri, Columbia.

Zhang, Q.F., W.N. Guan, Z.Y. Ren, and X.S. Zhu. 1983. Transmissibility of barley yellow dwarf virus strains from northwestern China by four aphid species. Plant Dis. 67:895–899.

Zhu, H., and Z.X. Guo. 1981. [Studies on causal factors of wheat scab and breeding for resistant cultivars]. Fujian Agric. Sci. Tech. 6:5–7.

Zillinsky, F.J. (ed.) 1983. Common diseases of small grain cereals: A guide to identification. Agribookstore, IADS Operations, Arlington, VA.

Ziv, O., J.M. Sacks, and Z. Eyal. 1981. Inheritance of tolerance to Septoria leaf blotch of wheat. Phytopathology 71:119–123.

9 Insect and Mite Pests of Wheat

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Wheat is a host of more than 100 species of arthropod pests that reduce grain yield and quality and increase production costs. In the USA alone, over 30 species of insects and mites attack wheat. The pest status of many of these species is well documented. Fortunately, most species are only occasional pests or inhabit limited areas. Only a few species are of major economic importance and cause severe damage over large geographical areas. Among the most destructive pests of wheat are the Hessian fly, *Mayetiola destructor* (Say); greenbug, *Schizaphis graminum* (Rondani); wheat stem sawfly, *Cephus cinctus* Norton; armyworm, *Pseudaletia unipuncta* (Haworth); army cutworm, *Euxoa auxiliaris* (Grote); grasshopper, *Melanoplus* spp.; and the brown wheat mite, *Petrobia latens* (Müller). Outbreaks of these pests have been recorded numerous times in the history of American agriculture. In the USA, insects and mites cause an estimated average annual loss of 6% of the total crop value. Also, indirect losses amounting to several million dollars annually are attributed to virus diseases transmitted by arthropods. In this chapter we discuss some of the more important field arthropod pests of wheat in North America, including their biology and life history, the nature of the damage they cause, and methods for their control. A few of the more serious field pests of wheat in other parts of the world are also included because of their economic importance to wheat production.

Most of the arthropod pests of wheat belong to eight major orders: Orthoptera, Homoptera, Hemiptera, Coleoptera, Lepidoptera, Diptera,

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and Hymenoptera (insects) in the class Insecta and Acarina (mites) in the class Arachnida. These pests attack the wheat plant in all stages of development, from seed germination to seed maturity. They either directly consume the vegetative and reproductive parts of the plant or suck the plant's fluids. Some pests inject toxic secretions into the plant as they feed, causing severe stunting or necrosis. A few pests are economically important only because they are vectors of pathogens.

Many of the arthropods that now live on wheat are indigenous to North America. Some species had restricted food habits and fed primarily on native grasses before wheat was introduced. Other species were polyphagous and fed on a variety of native plants. With the widespread cultivation of wheat, these arthropods readily adapted to wheat and have become pests. However, some of the more important pests, such as the Hessian fly, greenbug, and cereal leaf beetle, *Oulema melanopus* (L)., have been introduced from other countries. Since the natural enemies of introduced pests are usually left behind, the pests are often more destructive in their new environment than they were in their native lands. Several important pests of wheat are not known to occur in the USA; these include the sunn pest, *Eurygaster* spp.; wheat midge, *Contarinia tritici* Kirby; and the wheat bulb fly, *Delia coarctata* (Farlen). Even though there are strict quarantine laws to prevent their entry, foreign pests continue to be a serious threat to wheat production.

The insects and mites that attack wheat have complex biological systems, varied life cycles, diverse food habits and powers of dispersal, and different ecological requirements for survival. All of these life processes affect their distribution and activity. The reproductive rates of arthropods vary, but in general, most species have high reproductive potentials. Some species, such as the greenbug, may have many generations during a season, whereas some wireworms, *Ctenicera* spp., require several years to complete their life cycle. Many wheat pests have high survival potentials because they have long life spans as adults, are highly mobile, or can live on hosts other than wheat. The geographical distribution of a pest species is determined to a large extent by the pest's tolerance to adverse conditions. If the environment in a region is favorable to an insect with high biotic and survival potential, the insect may frequently become a serious pest.

9–1 NATURE OF LOSSES

Many physical and biological factors regulate the abundance and destructiveness of arthropods in wheat fields. Because of these factors, pest populations are constantly changing. Widespread outbreaks of pests tend to be periodic and are the exceptign rather than the rule. This period of abundance may last for only a few weeks, or it may continue for several years. Outbreaks may occur because of the nature of the pests' life cycle, but they are more often associated with favorable climatic or nutritional

factors or reduction of natural enemies. However, pest abundance is influenced more by weather than any other factor. Weather conditions may affect the density of a pest population directly or indirectly through their effects on its food, habitat, and natural enemies. Weather extremes may favor some pest species and be unfavorable for others.

Cultural practices may influence the distribution and abundance of arthropod pests. Continuous cropping of wheat over wide areas has created an ideal condition for increased pest abundance and damage. For pests that prefer wheat, such as the Hessian fly and the wheat stem sawfly, there is an opportunity for almost unlimited reproduction. Changing tillage practices will often change pest density and species composition. The effect of reduced tillage on wheat insects has not been studied extensively, but this expanding practice is expected to increase the abundance of certain pests. Increasing the amount of crop residue on the land not only reduces soil temperature and increases soil moisture, but also results in temperature fluctuations that are less extreme, and fields with heavy surface residue provide more winter protection and enhance the survival of some pests. Time of seeding also influences the vulnerability of wheat to pest attack. Early seeding of winter wheat exposes the crop to greater numbers of pests and allows some pests to complete additional generations.

An infestation of a pest species in a wheat field is not always a sign of an impending crop loss. Insect control is usually justifiable when the increase in yield is worth more than the cost of control. In the case of a low-unit-value crop such as wheat, the feasibility of controlling pests is difficult to determine. Ideally, two values must be known before a management decision can be made about control measures. The first is the *economic injury level*, which is the lowest population density of a pest at which economic damage can occur. Accurate economic injury levels are difficult to determine because several complex factors must be considered in their calculation, such as plant genotype and growth stage, density and developmental stage of the pest, weather, abundance of natural enemies, cost of control, and the market value of the crop. Crop and pest models that include all of these factors have not been developed. The second value that must be determined is the *economic threshold level*, derived from the economic injury level, which is the pest density at which control measures should be applied to prevent an increasing pest population from reaching the economic injury level. Suggested economic threshold levels for wheat have been published for major wheat-growing areas (Cuperus and Johnston, 1984).

The integrated pest management approach to insect control has received much emphasis since the early 1970s. The strategy of this approach is to employ and integrate all possible control methods for effective insect control, the objective being to maintain pest populations below the economic injury level with minimal adverse effects to crop ecosystems. A variety of control methods have been used in combination or singly for

effective integrated management of wheat arthropod pests. The major control techniques have utilized cultural practices, plant resistance, biological methods, and several types of chemicals. The major and potential uses of these four tactics in preventing or minimizing insect and mite damage to wheat are discussed in section 9–3.

9–2 ARTHROPOD PESTS

9–2.1 Sap-Sucking Arthropods

A diverse group of arthropods pierce and suck sap from the leaves, stems, and, less frequently, the developing kernels of wheat. These range from minute, gregarious mites to relatively large, solitary pentatomids. All of them rob the plant of moisture and nutrients, thereby adversely affecting both the quality and quantity of grain. Some inject toxic substances that destroy plant tissue. Some are vectors of viruses that may cause widespread losses, which may exceed those attributed to the direct feeding damage.

9–2.1.1 Aphids (Aphididae)

As a group, aphids are the most cosmopolitan insect pests of wheat. As an example, the greenbug is found in five continents, so its nativity is difficult to verify. Similarly, the English grain aphid, *Macrosiphum (Sitobion) avenae* (F.), and *Rhopalosiphum padi* (L.) are widely distributed in Europe and the Americas, and the corn leaf aphid, *R. maidis* (Fitch), is a pest in North America and Asia. Aphids are characterized as being highly mobile since the alate (winged) forms may ride in low level jet winds for 80 km or more. Sometimes even the apterous (wingless) forms are carried short distances by the wind. Aphids are noted for having high reproductive potentials. A female matures sexually in 1 to 2 weeks and can produce 20 to 100 young during an additional 3 to 4 weeks. There may be 10 to 15 overlapping generations during a growing season. Most aphids reproduce by apomictic parthenogenesis. This preserves heterozygosity and may be the basis for great adaptiveness; hence, the frequent occurrence of biotypes.

Over 30 species of aphids sporadically colonize wheat, but the greenbug, the English grain aphid, the corn leaf aphid, *R. padi*, the yellow sugarcane aphid, *Sipha flava* (Forbes), and recently the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), are the major ones in North America. Table 9–1 has brief descriptions and behavioral comments of these six species. All except the yellow sugarcane aphid are vectors of barley yellow dwarf virus (BYDV). The western wheat aphid, *Brachycolus tritici* Gillette, has the potential to cause losses in the northern Great Plains since it also injects a toxin. The Russian wheat aphid has caused extensive damage to wheat in South Africa (Walters et al., 1984) and may transmit

Table 9–1. Common aphids on wheat in North America.

Aphid species	Appearance (10× magnification)	Behavior
Greenbug, *Schizaphis graminum* (Rondani)	*Wingless*: body light green with dark green stripe down center of back. Tips of cornicles and legs and most of antennae black. *Winged*: body green and brown. One forked vein in front wing. Cornicles, legs, and antennae same as wingless.	Early infestations, on undersurface of lower leaves. Inject toxin(s) during feeding, causing yellow-red area at feeding site. First damage is often noticed as "greenbug spots" in the field with dead plants in the center of the spot. Cause more injury in proportion to their numbers than most other grain aphids.
English grain aphid, *Macrosiphum* (Sitobion) *avenae* (F.)	*Wingless*: body bright green; cornicle, legs, and antennae black. *Winged*: body bright green. Two forks in vein in front wing. Cornicles, legs, and antennae same as wingless.	Early infestations, but often numerous in wheat heads. Sometimes staggers when walking. Usually does not cause damage in southern USA, but may in northern USA and Canada.
Corn leaf aphid, *Rhopalosiphum maidis* (Fitch)	*Wingless*: ovoid, blue-green; usually with conspicuous dark blotches around bases of cornicles. *Winged*: body black. Two forks in vein in front wing.	Late infestations. Usually in whorls. Occasionally large numbers on seedling wheat during warm spells in the fall. Can cause economic damage in the South.

(continued on next page)

Table 9–1. Continued

Aphid species	Appearance (10× magnification)	Behavior
Rhopalosiphum padi (L.)	*Wingless*: body ovoid, olive-green with reddish spot on back at base of cornicles. *Winged*: body dark green and black. Tips of leg segments, tips of cornicles and antennae black. Two forks in vein in front wing.	Common on leaves of grains and certain grasses. Control usually not required. Honeydew often copiously produced.
Yellow sugarcane aphid, *Sipha flava* (Forbes)	*Wingless*: bright lemon-yellow with conspicuous rows of tubricales with hairs on dorsal abdomen. Cornicles no longer than wide. *Winged*: head, abdomen, and legs yellow with thorax light brown. Cornicles same as above. Two forks in vein of front wing.	A subtropical species with outbreaks about every 10 yrs. Injury similar to that of greenbug except plants more likely to be necrotic.
Russian wheat aphid, *Diuraphis noxia* (Mordvilko)	*Wingless*: light green, elongated spindle-shaped body with extremely short antennae and a characteristic projection above the tail. Cornicles very small. *Winged*: body similar to wingless, but darker color.	May be favored by drought conditions and warmer than usual weather. Injury very distinct.

a viral disease (Von Wechmar, 1984). This species has been found on wheat in Mexico in 1980 (Gilchrist et al., 1984). In March 1986, the pest was first detected in the United States in the Texas High Plains, and later in the same year less severe damage was reported in Colorado, Kansas, New Mexico, and Oklahoma. At this writing, information on the Russian wheat aphid in the United States is very sparse, but wheat and barley seem to be the preferred hosts, with rye and especially oats less suited as food plants. Systemic injury is characterized by purple- or white-streaked leaves, often trapped, and stunted, flattened plants. Feeding causes leaves to roll, and this reduces the effectiveness of contact insecticides and parasite search. Efforts are underway to locate sources of plant resistance. *Acyrthosiphon (Metopolophium) dirhodum* (Walker) is an important aphid on wheat in South America and to a lesser extent in Europe, and occasionally is found in North America, where it has not been reported to damage wheat (Ba-Angood and Stewart, 1980a), but can transmit BYDV. *Sitobion (Macrosiphum) miscanthi* (Takahashi) is a pest of wheat in the Far East and Australia, but not in the Western Hemisphere.

The greenbug has been a serious pest of small grains in North America since about the 1880s (Plate 9–1). In the 20th century, greenbug outbreaks have swept the Great Plains, frequently extending into the Canadian Prairies. In 1968, with the advent of a biotype that could withstand high temperatures, sorghum, *Sorghum bicolor* (L.) Moench, became an important summer host. However, biotypes of the greenbug are not confined to the Great Plains. In the eastern USA, there are biotypes that attack forage and turf grasses (Ratcliffe and Murray, 1983). There are also different biotypes outside North America. Arriaga et al. (1983) in Argentina, Lara et al. (1983) in Brazil, and Barbulescu (1980) in Romania have used resistance sources that differ from those in the USA. In the Great Plains biotype A probably was not the first one, since barley, *Hordeum vulgare* L., was considered a secondary host (Wadley, 1931), but by the 1950s barley was the preferred host (Dahms et al., 1955). Also, even though biotype E is the predominant one in the Great Plains in the mid-1980s, many potential biotypes are probably represented by small numbers of individuals in the agro-ecosystem, and these can prevail if endowed with an inherited competitive advantage (Mayo and Starks, 1974).

Though the greenbug can withstand relatively low temperatures, it seldom overwinters north of southern Kansas (Harvey et al., 1982). Reproduction can occur at temperatures between 10 and 33 °C, but the optimum is about 23 °C (Wood and Starks, 1972). The greenbug has been collected from at least 78 species of Gramineae (Dahms et al., 1954), so forage grasses and winter small grains in the South furnish an abundance of food plants for overwintering females. Greenbugs feed on the aerial portions of plants, but in the winter they may infrequently shelter below the soil surface on the crown of wheat. Soon after winter wheat breaks dormancy, alate greenbugs begin to migrate north. Some wheat areas have damaging infestations of greenbugs every spring, but wide-

spread outbreaks usually occur only every 5 to 10 yr. These can also be damaging to wheat seedlings in the fall. Within a field, greenbugs have an aggregated distribution (Kring and Gilstrap, 1983), and hot spots in wheat fields may become visible when plants are discolored or killed (Plate 9–2).

Like the greenbug, the English grain aphid reproduces mainly by parthenogenesis, and alate viviparae migrate northward each spring. However, it is less gregarious on leaves and is more commonly found on the wheat spike. Movement between plants also is common (Bakker and Robinson, 1975), and this behavior could increase the spread of BYDV. When the English grain aphid feeds on lower leaves, there is little measurable yield loss (Wood, 1965), but heavy infestations in the spikes at the time of flowering can significantly reduce grain yields (Rautapää, 1966).

A few males of the corn leaf aphid have been reported (Wildermuth and Walter, 1932), but reproduction and dispersal are similar to other wheat aphids. The northward movement of the corn leaf aphid lags behind that of the greenbug and English grain aphid (Kieckhefer et al., 1974). Infestations rapidly decline when the wheat leaves unfurl (Kieckhefer, 1975) and alate individuals move to summer hosts such as corn, i.e., maize (*Zea mays* L.), and sorghum. Fall infestations on seedling wheat can be a problem, but the aphids prefer barley at this time of year. Grewal and Bains (1975) found that a mix of 41 to 60% corn leaf aphid and *S. miscanthi* per wheat tiller caused a kernel weight loss of about 26%.

Rhopalosiphum padi, unlike most wheat aphids, alternates sexual and asexual reproduction on woody and herbaceous plants, respectively (Vickerman and Wratten, 1979). Even so, sexuparae are not believed to be important in the infestation of small grains (Kieckhefer et al., 1974). Movement northward precedes that of the corn leaf aphid. Feeding is mainly on lower leaves, especially during the warmer periods of the day. *Rhopalosiphum padi* in North America causes little damage in its southern range, but it can reduce the yield and protein level of wheat in northern regions (Ba-Angood and Stewart, 1980b). It is the most efficient vector of BYDV in North America.

The yellow sugarcane aphid is native to North America. Though first described in Illinois, it remains largely in the Gulf Coast states except for every 10 to 15 yr, when it moves northward in large numbers. During these outbreaks, damage to wheat can extend into the Missouri River valley. Like the corn leaf aphid, it prefers warm weather, but does not reproduce readily in low humidity. Buildup of infestations within a field is usually slow, but the aphid is difficult to control with insecticides, and even after treatment plants may remain stunted or die (Starks and Mirkes, 1979). Furthermore, the common aphid parasites do not prefer the yellow sugarcane aphid as a host. This species is not known to transmit a plant virus.

Because of unfavorable weather and the presence of biotic enemies,

wheat aphids do not reach their maximum distribution, potential reproduction, or consequential damage. Hard rains or blowing soil particles may dislodge some aphids, and these may emit a strong alarm pheromone that compels numerous others to drop to the ground. A large portion of these aphids will fail to relocate on plants. The greenbug fares poorly during extended periods of hot and dry weather after a severe winter (Rogers et al., 1972a).

Several native parasites and predators readily attack cereal aphids, though introduced beneficial insects have not had much impact (Rogers et al., 1972b). The most important parasite in the Southern Plains is *Lysiphlebus testaceipes* (Cresson), a small braconid wasp (Hight et al., 1972). Several species of predators feed on aphids. However, populations of beneficial insects lag behind the development of aphid infestations, so economic damage is frequently experienced before natural enemies effectively intervene.

The manipulation of cultural practices to control aphids on wheat has met with mixed success. Grazing winter wheat greatly reduces aphid numbers, but only temporarily. Good agronomic practices such as high soil fertility can stimulate the recovery of plants after greenbug attack, but may favor aphid population increases (Henderson and Perry, 1978). The type of cultivation affects greenbug populations; higher surface residues result in lower populations compared to conventionally tilled plots (Burton and Krenzer, 1985). The destruction of volunteer small grains and host grasses does little to control aphids or reduce the incidence of BYDV (Palival, 1982).

Several organophosphate insecticides give excellent control of aphids on wheat even though moderate resistance to these insecticides has been encountered (Teetes et al., 1975). In the spring, greenbugs frequently feed and multiply on wheat when temperature is around 10 °C. Foliar applications of insecticides under such conditions may give disappointing results, but Bauernfeind (1983) reported that malathion (*O,O*-dimethyl phosphorodithoate of diethyl mercaptosuccinate) was effective, and DePew (1982) concluded that several other insecticides gave control.[1] The decision to treat for aphids is determined by several factors, including the species and the number per plant.

New greenbug biotypes have hindered the development of greenbug resistant cultivars. But sources of resistance to the predominant biotypes have been discovered, and plant breeders are incorporating these sources into locally adapted wheats. Low but usable levels of resistance to the English grain aphid have been located in wheat cultivars (Lowe, 1983). Pubescent wheat cultivars are resistant to the English grain aphid (Markkula and Roukka, 1972) and *R. padi* (Roberts and Foster, 1983), but are not effective against the greenbug (Starks and Merkle, 1977).

9-2.1.1.1 Other Homoptera. Leafhoppers (Cicadellidae) and plant-

[1] Mention of a pesticide does not constitute a recommendation for use by the USDA, nor does it imply registration under FIFRA as amended. Mention of a proprietary product does not constitute endorsement by the USDA.

hoppers (Fulgoridae) are more commonly wheat pests in Asia than in North America. The green rice leafhopper, *Nephotettix bipunctatus* Uhl., damages wheat in several Asian countries. *Zyginidia quyumi* (Ahmed) is an economically important wheat pest in Pakistan (Jabbar and Ahmed, 1980). Leafhoppers seldom damage wheat in the USA, though Osborn (1932) listed six species that injure small grains. These have wide host ranges among cereals, forages, and weeds, with wheat often of secondary importance. Both leafhoppers and planthoppers are relatively small insects that readily hop or fly when disturbed. The overwintering stage depends on the species and the geographical area inhabited by the species. Eggs are inserted into plant tissue. There are four or five instars and as many as six generations during warm weather. Both nymphs and adults suck sap, and several species inject toxins that cause chlorosis. In addition, many species are the only known vectors of some small-grain pathogens.

Chemical control is seldom economical, but several insecticides are highly effective at relatively low dosages. Frequently infestations will suddenly disappear when wheat starts to head. Mowing adjacent grass and weeds can help to prevent damage in the margin of wheat fields.

9-2.1.2 Chinch Bugs (Lygaeidae)

The chinch bug, *Blissus leucopterus leucopterus* (Say), is usually considered a pest of maize and sorghum, although it occasionally damages wheat. It is native to North America, and occurs in the central and eastern USA. The adult is about 4 mm long and black with white wings. The egg is cream colored at first, but becomes red before hatching. The newly hatched nymphs are red and then darken as they mature. Both adults and nymphs have piercing-sucking mouthparts that take up plant fluids from the vascular system. If the bugs are abundant, they can severely stunt or kill wheat.

Chinch bugs overwinter as adults in bunch grasses, along fence rows, and in crop stubble. Females that survive the winter oviposit in small grains and grasses in the spring. Outbreaks are associated with mild winters and above-normal temperatures and below-normal rainfall between March and October. The first-generation bugs feed on small grains until the grain matures; then they migrate to other crops, usually corn or sorghum. There are two generations in the North and usually three in the South. Overwintering adults usually fly to areas of a grain field with thin stands, so management that results in thicker stands will help to minimize plant damage. Also, thick stands result in more humid conditions that enhance a fungal disease that can kill large numbers of bugs. Insecticides are not commonly used for chinch bug control on wheat.

Other members of Lygaeidae that attack wheat are *B. diploterus* Dist. in South Africa, *Nysius ericae* Schill. in Europe and North America, and *N. vinitor* Bergr. in Australia and North America (Bonnemaison, 1980).

9-2.1.2.1 Other Hemiptera. Stink bugs (Pentatomidae) possess

thoracic glands that emit strong odors. They have piercing-sucking mouthparts that form a slender, segmented beak. The southern green stink bug, *Nezara viridula* (L.), and the rice stink bug, *Oebalus pugnax* (F.), are occasional pests of wheat in the southern USA extending to Arizona. Further north, the Say stink bug, *Chlorochroa sayi* Stål, can cause yield losses when kernels are in the milk stage (Jacobson, 1965). At this stage of plant development, one adult per 10 spikes can cause sufficient loss in kernel weight and baking quality to justify control (Viator et al., 1983). Earlier feeding on leaves or later feeding on dough-stage kernels does not cause as much damage.

The sunn pest and cereal bug refer to several different species of *Eurygaster* (Scutelleridae) and *Aelia* (Pentatomidae). The sunn pest complex has not yet been found in the Western World (although other species of *Eurygaster* and *Aelia* are present). The most important species is *E. integriceps* Puton, which is found in eastern Europe and Asia (Paulian and Popov, 1980). While feeding, they secrete certain enzymes that affect the gluten of the grain and reduce the baking quality of the flour. Although losses caused by this insect vary, they are often greater than 25%. The use of early maturing cultivars has been suggested, since the sunn pest does little damage after kernels begin to harden. The use of organophosphate compounds is the principal control method. A density of one to three individuals of the sunn pest per m^2 is enough to justify control in a wheat crop with normal vegetation and density (Paulian and Popov, 1980). Because *Aelia* and *Eurygaster* spp. have a great potential for adaptation to new environments, they should be given serious attention in the Western Hemisphere.

Some species of plant bugs (Miridae) are occasional pests of wheat, but they appear to be more important in Europe than in North America. Plant bugs are rarely over 10 mm in length, are usually elongated and soft bodied, and are generally brightly colored. Species which are known to damage wheat include *Miris dolobratus* L., *M. ferrugatus* Fall., *Adelphocoris rapidus* (Say), *Stenotus binotatus* F., *Lygus pratensis* L., *Anapus freyi* Fieb., *Trigonotylus ruficornis* Geoff., *Orthocephalus brevis* Panz., and *Lopus infuscatus* Brullé (Bonnemaison, 1980).

9-2.1.3 Mites (Acari)

The four most common mites on wheat are the wheat curl mite, *Eriophyes tulipae* Keifer, the brown wheat mite, *Petrobia latens* (Müller), the winter grain mite, *Penthaleus major* (Dugès), and the Banks grass mite, *Oligonychus pratensis* (Banks). All are small and have two body regions. Typically, phytophagous mites have eight legs as adults, but the wheat curl mite has only four.

The wheat curl mite has a white, elongated body. It feeds on the upper leaf surface, where eggs are laid. The mite thrives in high humidity and reproduces at temperatures as low as 7 °C (Somsen and Sill, 1970). It is dispersed mainly by air currents. Feeding causes leaves to curl up-

ward toward the midvein, sometimes trapping subsequent leaves or spikes. The curl mite would be of minor importance if it were not the vector of the wheat streak mosaic virus (WSMV). Both the mite and the virus have a wide host range that includes small grains, maize, and several grasses (Slykhuis, 1953).

Among mites, the brown wheat mite causes the most direct injury to wheat in the USA in a region extending north into Nebraska and west through Utah. Rapid population buildup and subsequent injury are most pronounced in low-rainfall areas. Rains of 1 cm or more or irrigation can abruptly terminate an infestation (DePew, 1968). Damaged leaves change from a silvery cast to a scorched appearance. This stage of injury is usually reached during drought conditions, so cause and effect are difficult to determine. Adult mites are about 0.5 mm in diameter and have rounded, glossy, dark-colored bodies with yellowish legs. No males have been reported. Females lay 25 to 30 shiny white eggs at the base of plants, where the eggs oversummer. Eggs require moisture before development begins, and the incubation period is about 10 days. After hatching, the adult stage is reached in less than 2 weeks. Feeding may continue during warm periods throughout the winter. During the winter, bright red-colored eggs are laid, producing a spring generation of mites.

The winter grain mite is a cool weather pest, and seedling winter wheat is especially subject to injury in the western part of the USA. Damage is similar to winter-kill. The mite is not confined to wheat, however. It is found on five continents on other small grains, grasses, legumes, weeds, and even cool-weather vegetables (Streu and Gingrich, 1972). Adults are dark-brown to black, about 1 mm long. There are normally two generations per year. Development from eggs to adults takes about 2 months. Most feeding is done at night or during cloudy days. Temperatures above 24 °C terminate egg hatch and feeding.

The Banks grass mite is probably a species complex of cream-colored to yellow mites about 0.3 mm in diameter. It is the only prominent wheat mite that webs the leaves. All stages of the mite may be found within the webbing. Development from eggs to adults takes about 2 weeks, and adults live an additional 2 weeks. Leaves turn silvery at the tips and margins before becoming brown. Damage typically coincides with hot, dry weather after heading. Rain will quickly reduce populations. Conversely, insecticide treatments applied for pests such as aphids may be followed by a rapid build-up of mites with insecticide resistance (Ward et al., 1972).

Cultural control of mites has long been recommended. Destruction of host plants and delayed seeding of wheat reduce wheat curl mite populations; summer fallowing and irrigation lower the incidence of the brown wheat mite; and crop rotation is detrimental to the winter grain mite. Chemical treatment for mite control is seldom necessary, but several insecticides will give effective control.

9–2.2 Leaf-, Stem-, and Spike-Chewing Insects

In general, phytophagous insects with chewing mouthparts are relatively large and produce few generations per year. Many species are highly mobile and feed on a wide array of hosts. Also, many species are capable of widespread outbreaks triggered by poorly understood interactions of biotic and abiotic factors.

9–2.2.1 Cereal Leaf Beetle (Chrysomelidae)

The cereal leaf beetle, *Oulema melanopus* (L.), is one of the newer pests of North American wheat, having first been identified in southwestern Michigan in 1962. It is not known how this Eurasian chrysomelid became established in North America, but it has become a pest of wheat east of the Mississippi River. In 1984, the first major infestation west of the Mississippi River was found damaging small grains in Morgan Co., UT. A review of the cereal leaf beetle in North America (Haynes and Gage, 1981) and an extensive bibliography (Battenfield et al., 1982) have been published.

The adults are about 6 mm long (Fig. 9–1). The head and wing covers are metallic bluish black, and the legs and prothorax are orange. The yellow cylindrical eggs are laid singly or in small chains on the upper leaf surfaces. The larvae are yellowish, but shortly after hatch they become covered with a shiny black fecal coating. There are four larval instars.

The larval stage is usually the most destructive. The early instar larvae chew long narrow channels between the leaf veins and do not usually feed through the leaf. Thus, severely damaged leaves are translucent, and heavily infested fields may have the appearance of frost damage (Fig. 9–2). Winter wheat may escape serious injury because it often has extensive spring growth by the time overwintering beetles become active. Nevertheless, significant yield losses in winter wheat can occur, with grain losses ranging from 14 to over 25% (Gallun et al., 1967; Rademacher, 1967; Webster et al., 1982; McPherson, 1983).

The adults overwinter in small-grain stubble, along fence rows, in leaf sheaths and ears of maize, and under the loose bark of trees. They become active during warm days (about 10 °C) in the spring and feed on grasses and winter grains. After mating, females oviposit on these hosts and later infest spring-seeded grains. The larvae pupate in the soil at a depth of 2 to 5 cm. Each pupa is contained in a cell of soil and mucous-like substance. The summer adults emerge and feed on native grasses, maize, and late-seeded spring grains. After about 3 weeks of feeding, they seek overwintering sites. There is one generation per year.

Insecticides, such as malathion, azinphos-methyl {*O,O*-dimethyl *S*-[(4-oxo-1,2,3-benzotriazin-3(4*H*)-yl)methyl] phosphorodithioate}, and endosulfan (6,7,8,9,10,10-hexachloro-1,5,5a,6,9,9a-hexahydro-6,9-methano-2,4,3- benzodioxathiepin-3-oxide), are effective against the cereal leaf beetle if applied when eggs are common and small larvae are readily

Fig. 9–1 Cereal leaf beetle adult.

noticeable. Insecticide control is recommended when there is one larva per flag leaf on large plants or a combination of three eggs or larvae on small plants. Small parasitic wasps have been established for biological control. Two of these are *Anaphes flavipes* (Foerster), an egg parasite, and *Tetrastichus julis* (Walker), a larval parasite. The most efficient method of cereal leaf beetle control is the use of resistant wheat cultivars (Webster et al., 1982).

9–2.2.2 Armyworms and Cutworms (Noctuidae)

Several species of armyworms and cutworms attack wheat, but only a few are serious pests. Some species feed at the soil surface, while others feed underground. Other species have a climbing habit and are called *climbing cutworms*. Some species often have a marching or army habit and will move together in large numbers across fields, defoliating all grasses in their paths. The most economically important species are the armyworm, *Pseudaletia unipuncta* (Haworth); the fall armyworm, *Spo-*

Fig. 9–2. Wheat damaged by cereal leaf beetle (*right*) and resistant pubescent-leaved cultivar (*left*).

doptera frugiperda (J. E. Smith); the wheat head armyworm, *Faronta diffusa* (Walker); and the army cutworm, *Euxoa auxiliaris* (Grote).

Armyworm moths are tan with a wing expanse of about 3.5 to 4.0 cm. The front wings have a white dot near the center. The moths are nocturnal and lay their eggs in masses in tight places such as the narrow space between the leaf sheath and stem. Females also oviposit on narrow blades of grasses, but afterwards they usually fold the leaf lengthwise, causing the two edges to stick together. The eggs are extremely difficult to find in the field.

Partially grown larvae that have overwintered can damage wheat early in the spring, but the most serious damage occurs at the time of heading, when larvae feed on the leaves and later on the kernels. Often the heads are completely severed from the stems, causing extensive grain loss. The larvae complete development in 3 to 4 weeks and pupate in the soil. The moths emerge in about 10 days and begin ovipositing. There are usually three to four generations per year. Even though the larvae are difficult to detect because they hide in the soil during the day, fields should be checked often, since small larvae are easy to control with insecticides. In most regions, three to four armyworms per 31 cm of row is considered the economic threshold. A sequential sampling method has been developed to estimate armyworm populations in wheat and barley (Coggin and Dively, 1982). Several natural enemies, including parasitic insects, are effective in reducing armyworm populations.

The fall armyworm is not a serious pest of wheat in the Great Plains,

but it occasionally damages early fall-seeded wheat in the South. A distinguishing feature of fall armyworm larvae is a light-colored, inverted Y-shaped suture on the head. The habits are similar to those of the armyworm. Since the fall armyworm attacks winter wheat during the seedling stage, a few larvae per unit area can do extensive damage. For seedling wheat, the economic threshold is two to three larvae per 31 cm of row. For larger plants, three to four larvae per 31 cm and noticeable feeding damage will justify an insecticide application.

The wheat head armyworm is an occasional problem on the heads of wheat and developing kernels, especially in areas where lodging has occurred, but control is rarely necessary. The moth has yellowish gray front wings with a broken chocolate-brown streak from the base to the tip; the hind wings are light brown. The wingspread is 2.5 cm.

The army cutworm is a sporadic pest in the western Great Plains, extending northwest to Oregon and north into Saskatchewan and Alberta in Canada. It can be very devastating in outbreak years. In Oklahoma alone, insecticides for armyworm control were applied to 1 012 500 ha during the 1976 outbreak (Burton et al., 1980). The grayish or dull brown moth prefers winter barley to winter wheat for oviposition, but it will also lay eggs in bare soil. Oviposition occurs in the fall. Each female lays 1000 to 3000 eggs, which explains the outbreak potential of this pest. The larvae are pale grayish with white splotches and usually with a pale mid-dorsal stripe. They feed on practically any herbaceous vegetation, usually at the soil surface, but will feed on plants below the surface after the aboveground portions have been consumed. They overwinter as partially grown larvae and become active in the spring when plant growth resumes. They will also feed when the temperatures are slightly above freezing, and cause extensive damage to winter wheat. A severely damaged field appears as if it has been closely grazed.

An economic threshold of two army cutworm larvae per 31 cm of row in wheat is suggested, depending on the growth stage of the plants and the size of the larvae. A 34% grain loss occurred in Oklahoma when there were 12 larvae per 31 cm of row (Burton et al., 1980). However, plants in good growing condition with 12 to 15 cm of top growth can withstand 32 to 43 larvae per m^2.

The larvae pupate in the soil, and the moths emerge in May or June. A large number of the moths in the Great Plains migrate to the higher elevations of the Rocky Mountains in the summer and then return in the fall. Further north, many adults also estivate in debris, under clods, or in cracks of buildings. There is one generation a year.

Natural enemies usually keep the populations below economically damaging levels, but insecticides are a necessity during outbreaks. Some of the more effective insecticides have been severely restricted or banned because of environmental hazards.

9-2.2.3 Grasshoppers and Crickets

Grasshoppers and crickets that attack wheat belong to three families of Orthoptera, but they share insatiable appetites on a wide array of host

plants and have similar life cycles. Over 600 species of grasshoppers attack cultivated crops in North America, but only five species cause about 90% of the damage. These prominent species are the migratory grasshopper, *Melanoplus sanguinipes* (F.), the differential grasshopper, *M. differentialis* (Thomas), the two-striped grasshopper, *M. bivittatus* (Say), the red-legged grasshopper, *M. femurrubrum* (De Geer), and the clear-winged grasshopper, *Camnula pellucida* (Scudder). The migratory grasshopper occurs throughout the USA and from Nova Scotia into Mexico, and is the most damaging species to wheat. It is especially destructive to seedlings of winter wheat. The two-striped grasshopper and the red-legged grasshopper share similar widespread geographical distributions, whereas the differential grasshopper is more southern and the clear-winged grasshopper is more northern in habitat. Parker (1954) gave an excellent review of grasshoppers.

No agricultural area in North America escapes grasshopper damage, but the most severe attacks are associated with annual precipitation of about 25 to 75 cm. Both nymphs and adults chew stems and leaves of wheat plants. Defoliation may be especially severe at the edges of fields bordered by roadways or drainage ditches. Damage is most pronounced when grasshoppers sever the spikes or feed on ripening kernels of wheat. In the past, grasshoppers have been associated with famine, since many species thrive during drought periods and vast migrating swarms can denude the countryside. For example, in Montana in 1938, Mills (1939) reported swarms up to about 5 km long and 305 m high, with population densities of 600 per m^2. Mathematical models have been developed for assessment of crop loss caused by grasshoppers (Gage and Mukerji, 1978).

Most of the economically important species of grasshoppers have one generation per year, but some have two or even three in warmer regions. Egg pods containing 5 to 100 overwintering eggs are placed 2 to 5 cm below the surface of the ground. Depending on climatic conditions, the eggs hatch from April until mid-June. Grasshoppers have four to six nymphal instars and become adults in about 6 weeks.

For the grasshopper there are many perils between the egg and adult stages. Numerous enemies including other insects and vertebrates prey upon grasshoppers. However, weather probably has the greatest influence on grasshopper abundance. Dry warm spring weather favors survival, but cool damp spring weather delays hatching and promotes a higher incidence of disease. One of the disease organisms, *Nosema locustae* Canning, has been developed into an applied control adjunct for grasshoppers (Onsager et al., 1981) and will infect at least 55 species.

Presently, conventional insecticides are still the mainstay for controlling outbreaks. Treatments are often directed toward rangeland habitats before migrating swarms move into wheat or other cultivated crops, or before egg laying begins. Cultural control practices such as plowing and disking destroy eggs and food plants for small nymphs. Trends toward minimum tillage could favor grasshopper survival.

Crickets are also sporadic, but occasionally devastating pests of wheat. Perhaps the most notorious species is the Mormon cricket, *Anabrus simplex* Haldeman, especially in Idaho, Montana, and Utah. Further northwest the coulee cricket, *Peranabrus scabricollis* (Thomas), behaves similarly to the Mormon cricket since individuals aggregate and move in swarms into cropland. Field crickets, *Gryllus* spp., also include wheat in their large selection of food plants, but seldom cause economic damage. Control measures for crickets are similar to those for grasshoppers.

9–2.2.4 Other Chewing Insects

Thrips (Thripidae) are dusty-colored, fringed-winged insects that seldom exceed 2 mm in length. Thrips damage is more often associated with horticultural crops than with wheat. However, several species, especially the western flower thrips, *Frankliniella occidentalis* (Pergande), feed on small grains and grasses. Typically, chloroplasts are destroyed, thus causing silvery streaks on the foliage. Spikes and developing kernels may also be injured. Most species complete their life cycle in 12 to 30 days, so there may be 10 to 15 generations per year. Wheat infestations are usually not sufficiently severe to justify control, but at least two insecticides, parathion (*O-O*-diethyl *O-4*-nitrophenyl phosphorothioate) and methyl parathion (*O-O*-dimethyl *O*-4-nitrophenyl phosphorothioate), are labeled for use.

Flea beetles (Chrysomelidae) may skeletonize leaves along the edge of wheat fields. Injury is often worse during cool damp springs. Adult blister beetles, *Epicauta* spp. (Meloidae), can quickly defoliate wheat, but damage is seldom extensive, since the beetles prefer other hosts. Ants (Formicidae) frequently forage in the edges of wheat fields. The most common invader is the red harvester ant, *Pogonomyrmex barbatus* (F. Smith), but its economic importance to wheat has not been determined. Imported fire ants (*Solenopsis* spp.) in the southern USA build mounds up to a meter in height, and these may cause harvesting difficulties. There are many other insects with chewing mouthparts that frequent wheat fields in small numbers, but they rarely cause economic damage.

9–2.3 Stem-Feeding Insects

Stems of wheat plants provide a nutritious food source and a protective habitat for insects. Several important insect pests attack the stems from the time plants are in the early jointing stage to physiological maturity. They may kill the plants outright or cause severe stunting that reduces both grain yield and quality. Infestations of stem-feeding insects, especially those that feed internally, are usually difficult to detect and control.

9–2.3.1 Hessian Fly (Cecidomyiidae)

The Hessian fly, *Mayetiola destructor* (Say), is one of the most destructive insect pests of wheat. The original home of the Hessian fly was

possibly in the southern Caucasus region of Eurasia. The insect has now spread to almost all principal wheat-growing areas of the world. It was first found infesting wheat on Long Island, NY, in 1779 and was believed to have been introduced in straw bedding used by the Hessian soldiers during the Revolutionary War. The Hessian fly now damages wheat over a wide region in the USA from the Atlantic coast to the Great Plains. It is also found along the Pacific coast in parts of California, Oregon, and Washington. It was not detected in eastern Washington until the late 1960s (Pike and Antonelli, 1981). Widespread outbreaks have occurred at irregular intervals, while local outbreaks cause extensive crop losses nearly every year. Damage estimated at $100 million in a single year has been caused by the insect (Cartwright and Jones, 1953).

Wheat is the preferred host of the Hessian fly, but it also infests barley and rye (*Secale cereale* L.). However, it is usually not a serious pest of these crops, though occasionally barley is heavily infested in some areas (Pike and Antonelli, 1981). Oat (*Avena sativa* L.) is not a host of the fly. Several wild grasses are alternate hosts when wheat is not available, such as: quackgrass, *Elytrigia repens (L.)* Beauv.; western wheat grass, *Agropyron smithii* Rydb.; rye grasses, *Elymus virginicus* L. and *E. canadensis* L.; little barley, *Hordeum pusillum* Nutt.; and goatgrass, *Aegilops* spp.

The adult Hessian fly is a small gall midge, darkish gray to black in color, and about 3 mm long. The egg is glossy red, cylindrical, and about 0.5 mm long. The first-instar larva is also red, but turns white within a few days. The full-grown larva is vermiform, greenish white, and about 4 mm long (Fig. 9–3, *left*). The puparium, commonly called flaxseed because of its resemblance to the seed of flax, is dark brown and 3 to 5 mm long (Fig. 9–3, *right*).

Injury by the Hessian fly is caused entirely by the larva, which sucks juices from the plant. Both the vegetative and reproductive stages of wheat are attacked. On young plants the larva feeds between the leaf sheaths near the crown of the plant. Infested tillers show a characteristic stunted appearance and have shorter, more erect, and darker green leaves than noninfested plants. In severe infestations, many of the young plants die, although some may develop new tillers. Heavily infested fields show areas of dead plants and thin stands. On older plants in the jointing stage, the larva feeds just above the node between the leaf sheath and stem. Feeding causes injury that prevents normal elongation of internodes and transport of nutrients to the developing head, which reduces both grain quantity and quality. The most obvious damage occurs when infested stems break over about the time plants mature (Fig. 9–4). Much of the grain of broken stems is lost when the crop is harvested.

In winter wheat, the typical life cycle of the Hessian fly begins with fall emergence of adults from infested wheat stubble or volunteer wheat. The fly is short lived and dies within a few days after emergence. The female oviposits on the upper leaf surface of young plants and lays between 200 and 300 eggs. The eggs hatch in 3 to 10 days, depending on

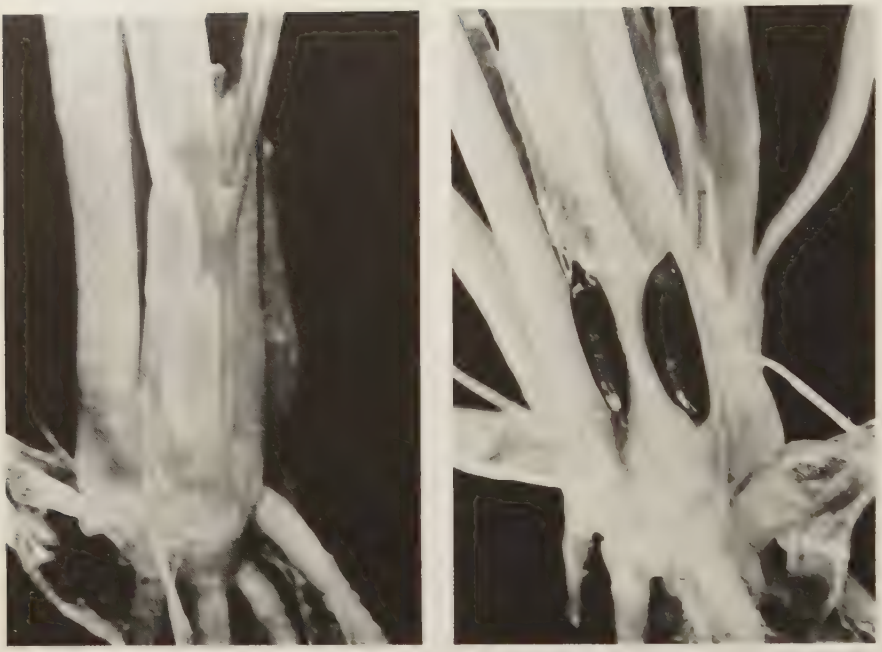

Fig. 9–3. Hessian fly larvae (*left*) feeding on seedling wheat and puparia or "flaxseeds" (*right*). Courtesy, Washington Agricultural Experiment Station, Prosser.

temperature. Newly hatched larvae crawl behind the leaf sheaths and migrate to the crown of the plant where they begin to feed. The developmental period of the larval stage varies, but most larvae become full grown before the onset of cold weather. When the larva is full grown, the outer skin hardens and forms a protective puparium (flaxseed). The larva passes the winter within the puparium. The following spring, these larvae pupate, and adults emerge and infest wheat about the time the plants begin to joint. Most of the larvae of the spring generation are found just above the nodes under the leaf sheaths. The larvae pass the summer inside the puparia in the dry stubble. In late summer or fall, the larvae pupate, and adults emerge and infest volunteer or early seeded wheat. In northern winter wheat areas, only two generations are normally produced each year, although supplementary broods may develop either before or after the main fall generation or after the main spring generation. In the northern spring wheat areas, there is usually only one annual generation in the spring.

Many physical and biological factors affect the abundance and destructiveness of the Hessian fly. When these factors favor the insect's survival and development, populations may increase rapidly. Consequently, when or where economic infestations may be imminent is not always predictable. Thus, control methods for the Hessian fly are mostly preventive rather than remedial. The three most important methods for preventing infestation are the use of resistant wheat cultivars, delayed

Fig. 9–4. Wheat damaged by the spring generation of the Hessian fly.

seeding of winter wheat to escape fall infestation, and the destruction of volunteer wheat. Resistant cultivars provide the most reliable and economical control. When resistant cultivars are not used, fall infestation can be reduced by delaying wheat seeding until most of the flies have emerged and died. The destruction of volunteer wheat is important in preventing the buildup of flies in late summer. The combined practices of delayed seeding of wheat and good management of volunteer wheat are highly effective in reducing infestations in winter wheat. Chemical control of the Hessian fly is seldom used in the USA.

9–2.3.1.1 Other Cecidomyiidae. Wheat is host to three other cecidomyiids: the saddle gall midge, *Haplodiplosis equestris* (Wagnner), and the wheat midges *Sitodiplosis mosellana* (Gèhin) and *Contarinia tritici* Kirby.

The saddle gall midge is found throughout Europe and the southern USSR. It does not occur in the USA. It also attacks barley, rye, and oat crops. The adult is slightly larger than the Hessian fly. The larva is red and about 4 to 5 mm long when full grown. Larvae feed behind the leaf sheaths on the stems. Gall-like swellings form around the larvae, leaving saddle-shaped depressions along the stem. Heavy infestations prevent heading and reduce grain yield. Injury is more severe in wet seasons, when many of the infested stems rot before the heads emerge (Barnes, 1956). Spring-seeded wheat is more heavily attacked than fall-seeded

wheat. The insect has one generation each year. Cultural practices such as crop rotation and plowing under crop residue are effective control measures. Insecticides have given good control and are used in some countries (Bonnemaison, 1980).

Sitodiplosis mosellana is found throughout most wheat-growing areas of Europe and the USA, and in parts of Canada. It also occurs in the USSR, China, and Japan (Barnes, 1956). This midge, believed to be a native of Europe, was found in North America in Quebec in the early 1800s. Outbreaks of the pest on wheat in the USA are infrequent, although serious losses have been reported, mainly in northeastern states. Wheat appears to be the preferred host, but the insect has been reported on barley, rye, and oat crops. Larval feeding causes shriveled or shrunken kernels, although the injury also allows the entry of fungi that further reduce seed quality. A positive association of *Septoria* glume blotch and midge larvae has been reported (Wellso and Freed, 1982). The wheat midge has one generation each year. The small mosquito-like flies emerge about the time wheat begins to head. The orange-colored eggs are usually laid singly within a floret just under the edge of the glume. The larvae feed on the surface of the developing kernels, and complete their development in about 3 weeks. When full grown, they crawl out of the florets and drop to the soil to overwinter. The following spring, the larvae pupate in the soil and give rise to adults of the next generation.

Contarinia tritici is found throughout Europe, in the USSR, and in Japan. It is considered a serious pest of wheat in Europe, but its pest status in other countries is not known. This species is sometimes confused with *S. mosellana*, since both are similar in size and appearance and both attack the florets of host plants. In some areas, the two species frequently occur in the same crop, often in the same head. *Contarinia tritici* also infests barley and rye, but the preferred host crop may depend on the flowering stage of the host at the time adults are active. *Contarinia tritici* has one main generation in the spring and a partial generation in the fall. Eggs are laid in clusters within florets on the inner surface of the glumes. Larvae feed on the young embryo, which is eventually destroyed, producing a sterile floret. The larvae complete their development in about 3 weeks and drop to the ground to pupate. Control of both *C. tritici* and *S. mosellana* may be necessary when heavy infestations are expected. Under certain conditions, different tillage methods in the fall and spring may be effective in destroying larvae in the soil. However, insecticides applied at heading are sometimes required to prevent egg laying (Bonnemaison, 1980).

9-2.3.2 Wheat Stem Maggots (Chloropidae)

The wheat stem maggot, *Meromyza americana* Fitch, is native to North America and widely distributed through wheat-growing areas from Mexico to Canada. Two other species, *M. pratorum* Meigen and *M. saltatrix* (L.), with similar life histories occur in the Pacific Northwest (Rock-

wood et al., 1947). Serious outbreaks of *M. pratorum* and *M. saltatrix* have occurred on wheat in Europe and Asia. *Meromyza americana* is considered the most important of the three species in the USA. In infested fields, it is common to find 10 to 15% of the plants injured by this insect. In addition to wheat, the principal host crops are barley and rye. It also feeds on numerous native and introduced grasses.

The adult is a slender, pale green to yellow fly, about 6 mm long. It has three broad grayish black stripes on the mesonotum and three brown stripes on the dorsum of the abdomen. The egg is white, cylindrical, and about 1 mm long. The larva is a slender, pale green maggot about 6 mm long when full grown.

The wheat stem maggot attacks both spring and winter wheat and causes two types of injury. When young tillers are attacked in the fall or early spring, the central shoot is cut off by the larva feeding inside the tiller. The shoot withers and turns yellow, and the tiller eventually dies. Heavy infestations may cause severe reductions of wheat stands. The other type of injury occurs in late spring and early summer when the larva feeds inside the stem, usually in the peduncle, and prevents the normal flow of sap to the developing head. This injury causes the head to die prematurely and turn white before the kernels are formed. The wheat stem maggot normally has three full generations each year: one in the spring, a second in early summer, and a third in early fall that overwinters as larvae at the base of infested tillers. Although damage by wheat stem maggot can be locally severe, the insect seldom causes widespread economic damage. There is no satisfactory control method for preventing damage, although cultural practices, such as crop rotation, clean cultivation, and late seeding of winter wheat, will reduce infestations. The spring generation injures early-maturing cultivars less than late-maturing ones (Allen and Painter, 1937). Branson (1971) found that adults prefer to oviposit on wheat cultivars with the greatest number of tillers.

9-2.3.2.1 Other Chloropidae. Frit flies, *Oscinella* spp., are important pests of oat and other cereal grains over extensive areas of Europe, though they are of minor importance in North America. Several species attack cereals, but *O. frit* (L.) is considered the most serious one. In Europe the preferred host is oat crops, but in North America wheat is preferred (Aldrich, 1920). *Oscinella frit* is widely distributed in the USA, although it is more abundant in winter wheat areas of north-central and eastern states. It also attacks barley, rye, oat, maize, and several other wild and cultivated grasses.

Adults of the frit fly are black, 1 to 2 mm long. Eggs are minute, white, and elongate. When first hatched, larvae are whitish, becoming yellow when full grown. There are normally three generations each year. Eggs may be laid on any part of the plant. In the fall, the first-generation larvae mine the leaves of young plants; later they bore into the stems and feed on the embryonic growing point of the shoot. Larvae overwinter

within the stems and pupate in early spring. In the spring and early summer the second- and third-generation larvae feed on the developing spike, causing sterility. Spring cereals are more seriously affected by infestations than winter cereals.

Control of the frit fly in wheat is seldom practiced in the USA. Injury to winter wheat can be reduced by destroying weed grasses and volunteer cereals in the fall and by late seeding. Spring cereals should be seeded as early as practicable to minimize damage by the spring infestations. In Europe, seedling protection is sometimes needed, and several insecticides are recommended (Bonnemaison, 1980).

The gout fly, *Chlorops pumilionis* (Bjerkander), is an important pest of spring and winter wheat in some areas of Europe. It occurs throughout Europe and the USSR. The insect also attacks barley, rye, and grasses, especially quackgrass. Normally there are only two generations each year, although a small third generation may develop in the fall. The type of injury depends on the growth stage of wheat. When young plants are infested, the tillers are stunted, swollen in shape, and fail to produce spikes. Damage by the spring-generation larvae is usually 2 or 3 weeks before heading. The larvae feed in the upper internode and eat a groove down the side of the spike to the first node. This injury reduces the growth of internodes and the number, quality, and weight of kernels. Control of the gout fly is largely by preventive measures. Damage is minimized if both early and late seedings are avoided (Lilly, 1947). Clean cultivation of cropland infested with wild grasses is important in preventing infestations.

9-2.3.3 Wheat Bulb Fly (Anthomyiidae)

The wheat bulb fly, *Delia (Hylemya) coarctata* (Fallen), occurs mainly in central and northern Europe, parts of the USSR, and Manchuria. It is primarily a pest of fall-seeded wheat, rye, and barley. The main wild host is quackgrass. The insect has been identified in eastern Canada and northeastern USA (McAlpine and Slight, 1981), but there have been no reports of damage to wheat.

The adult fly resembles a house fly, but is slightly smaller. In Great Britain, eggs are laid during the late summer in fallow soil or in root crops and hatch during late winter and early spring (Gair and Maskell, 1982). The newly hatched larvae die unless the field has been seeded to wheat, barley, or rye, or unless host grasses are present. The young maggots are white and about 1 mm long. They bore into the seedling below ground at the bulb, or base, of the stem. Within a few days, feeding causes the central shoot to wither and turn yellow. Maggots that feed in large shoots can complete their development in one shoot, but they often move from shoot to shoot on the same or different plants. When full grown, the creamy-white maggots are about 10 mm long. This stage is usually reached during April and May, when the maggots pupate in the soil. The

adults emerge in late spring and early summer. Only one generation per year is produced.

The amount of damage to the crop depends on several factors, such as the population of maggots and the stage and vigor of the crop. Where late seeding and unfavorable weather delay germination, seedlings may be attacked and killed before they emerge. Damage can be reduced effectively by cultural methods. Wheat that is well established by the time infestation occurs is better able to withstand attack. Thus, early seeding with an increase in seed rate is the best control measure. However, early sown crops produce more tillers, which may increase survival of the maggots. Control also can be obtained by a change in crop rotation, since the insect occurs only in fallow soil or in root crops. Although no chemical control is completely effective against the maggots, certain insecticides applied as a seed, granular, or spray treatment can give useful protection.

9-2.3.4 Sawflies (Cephidae)

Three species of sawflies are economically important pests of wheat in North America: the wheat stem sawfly, *Cephus cinctus* Norton; the European wheat stem sawfly, *C. pygmaeus* (L.); and the black grain stem sawfly, *Trachelus tabidus* (F.). *Cephus cinctus* is native to North America and is widely distributed in the USA west of the Mississippi River and in parts of Canada. However, it is most destructive in the northern Great Plains wheat-producing areas of the USA and Canada. *Cephus pygmaeus* and *T. tabidus* are native to Europe and inhabit about the same area in the Eastern Hemisphere. Both species occur mainly in the eastern USA. Wallace and McNeal (1966) gave a complete account of the importance, distribution, biology, and control of the three species. The appearance, life history, and type of damage of all three species are similar. Since the wheat stem sawfly occurs in the more intensive wheat-growing areas of North America, it is the most serious pest of the three species. Thus, only this species will be discussed.

The wheat stem sawfly has a wide range of hosts, including nearly all of the cultivated cereal grains, although wheat is preferred. Females will deposit eggs in oat, but larvae fail to develop. Several native and introduced grasses also serve as hosts. *Elytrigia* grasses probably were the preferred hosts prior to commercial production of wheat.

The adult wheat stem sawfly is a slender, black and yellow wasp, about 9 mm long. The eggs are small, crescent-shaped, and white. Larvae are legless, pale yellow, and about 12 mm when full grown. Sawfly injury to wheat is caused solely by the larvae. The larvae tunnel inside the stem, which interferes with nutrient transfer and weakens the stem. This injury causes smaller and lighter kernels (Salt et al., 1945). The larvae also girdle the stem at the base when preparing for overwintering. Girdled stems break off and fall to the ground. Most of the spikes of broken stems are lost.

The wheat stem sawfly produces one generation a year. Adults emerge

from the stubble of the previous wheat crop from mid-spring to early summer, depending on latitude. Females thrust their eggs into the hollow portion of the growing wheat stems. Eggs hatch in 7 to 10 days, and the larvae begin to tunnel up and down, feeding on the pith of the stem. The larvae are cannibalistic, and only one survives in a stem. The larva completes its feeding by late summer and moves to the lower part of the stem and cuts a V-shaped groove around and inside the stem. The larva plugs the stem with frass below the cut and constructs a chamber in which it overwinters and pupates the following spring.

Control of the wheat stem sawfly is difficult, since the eggs and larvae are inside the stems. Insecticides have not been recommended. Although many parasites attack the larva, biological control has not been successful. Deep fall plowing, spring disking, and crop rotation are effective in reducing populations, but these practices may not be compatible with other management practices. The use of solid-stem wheat cultivars that inhibit the development of the larvae is the best means of control. Several solid-stem cultivars have been developed and are presently grown in the USA and Canada.

9–2.3.5 Wheat Jointworm (Eurytomidae)

The wheat jointworm, *Tetramesa tritici* (Fitch), is found in most wheat-growing areas of the USA, but is a more serious pest east of the Mississippi River and in the Pacific Northwest (Phillips and Poos, 1940). Wheat is the only known host. At one time this insect ranked next to the Hessian fly in destructiveness to wheat. In recent years, however, there have been few reports of widespread damage.

The adult is a small black wasp, about 5 mm long, with yellow legs and transparent wings. The egg is minute, white, and bulblike. The larva is yellowish and about 6 mm long. The pupa at first is pale yellow, but gradually turns black. Injury to wheat occurs when larvae feed within the stem on the inner walls, causing the formation of small galls. These galls interfere with the transport of nutrients and prevent full development of the kernels. Infested stems also become malformed and are weakened above the galls, which cause many of the stems to break before harvest. The insect has one generation each year and passes the winter in the pupal stage. Adults emerge in the spring about the time wheat begins to head. Eggs are laid in the stem tissue just above the nodes. Feeding by the larvae causes distinct gall tissue to form around them. Larvae feed inside the galls and reach maturity in about 3 weeks. They remain in the stubble after the wheat is harvested and pupate inside the hardened galls in late fall.

In areas where it is practical, the wheat jointworm can be controlled by plowing under the stubble late in the summer or early in the fall to prevent emergence of adults. Also, good stands of vigorously growing wheat are injured less than poorer stands. In some years, several parasites

of the jointworm are effective in reducing the numbers of the pest. Insecticides have not given effective control.

9-2.3.6 Wheat Strawworm (Eurytomidae)

The wheat strawworm, *Tetramesa grandis* (Riley), is widely distributed throughout the USA and probably occurs wherever wheat is grown. This insect attacks only wheat and was once regarded as a major pest causing losses exceeded only by the Hessian fly and the wheat jointworm (Phillips and Poos, 1953). During the 1920s, this insect caused major economic losses in Kansas, and thousands of hectares were again damaged in the late 1940s. Although no recent outbreaks of the wheat strawworm have occurred, significant yield losses have been reported in limited areas (Martin and Harvey, 1982).

The wheat strawworm produces two generations per year, each of different morphological forms. The adult of the spring form (*minuta*) is about 2 mm long, wingless, and brownish, whereas the adult of the summer form (*grandis*) is much larger, winged, and black. The eggs are very small, white, and bulblike. The larva of the spring form is pale yellow, robust, and about 4 mm long when full grown. The larva of the summer form is similar in color, but is longer and more slender than the spring form.

Larvae of the spring and summer forms cause two distinct kinds of injury. The larvae of the spring form feed within and near the base of the young plant and destroy the developing spike. The larvae of the summer form feed within the stems of older plants just above the nodes. The stems are not killed and show no external evidence of injury, although both grain yield and quality are reduced.

The larvae of the summer form pass the winter as pupae in the wheat stubble. The first-generation adults (spring form) emerge in the spring, and females deposit their eggs within the tillers of young plants. The larvae feed on the central shoot and complete their development in 3 to 4 weeks. Larvae pupate within the tillers, and adults of the summer form emerge about the time wheat is in bloom. No males of the summer form have been found, and females reproduce without mating. Females deposit eggs singly in the stem, slightly above the nodes. Normally only one larva is found at a node. The larva feeds on young stem tissue and attains full growth before the tissue has hardened. The larva then forms a small cell within or near the node, where it pupates and overwinters.

Since the adults of the spring generation are wingless, the most effective control is to avoid growing wheat close to wheat stubble. Destruction of volunteer wheat is important, since the plants serve as a host for the spring generation. When compatible with other management practices, plowing the stubble under will prevent emergence of adults. Early maturing cultivars of winter wheat tend to escape infestation by the summer generation (Martin and Harvey, 1982).

9–2.3.7 Lepidopterous Borers

Several lepidopterous larvae that bore in the stems of plants are occasional pests of wheat. The two most injurious to wheat are the stalk borer, *Papaipema nebris* (Guenée), and the lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller). The stalk borer is distributed throughout the USA east of the Rocky Mountains. The larvae attack a wide variety of plants, but prefer giant ragweed (*Ambrosia trifida* L.) and maize during late larval instars. The insect has one generation a year and overwinters in the egg stage on numerous weed hosts. The young larva is a small brownish caterpillar with a continuous white stripe down its back. The mature larva is about 3 cm long and creamy white. The larva usually bores into the lower part of the stem and tunnels upward. The wheat spike fails to develop grain and turns white or yellow, while the leaves and stem remain green. Damage is seldom severe enough to require chemical control, since infestations are usually confined to field margins where larvae have migrated from weeds. The best method in preventing damage is a thorough cleanup of crop refuse and destruction of weed hosts in field margins during the fall.

The lesser cornstalk borer is primarily a pest of maize, although in the southern wheat areas of the USA it sometimes attacks early-seeded winter wheat. The insect occurs throughout the southern half of the USA, Mexico, Central America, and the northern half of South America (Dahms, 1967). There may be four or more generations a year. The mature larva is about 2 cm long and bluish green with conspicuous brown longitudinal stripes. The larvae may feed at first on lower leaves, but later bore into the plant and feed in the crown near the soil surface. The injury usually kills the plant or tiller. The insect is more troublesome on dry sandy soils. Wheat seeded at the recommended time usually escapes infestation.

9–2.4 Soil Insects

Soil-inhabiting insects are sometimes serious or potentially destructive pests of wheat. The larvae of these insects attack the germinating seeds, roots, and underground portion of stems. Most soil insects that attack wheat feed on a wide range of host plants. Infestations are difficult to anticipate and often go unnoticed until the crop is severely injured. Loss of stand is the common symptom of soil-insect feeding. The amount of damage usually depends upon soil type, tillage operations, crop rotation schemes, dates of seeding, and soil moisture conditions. In the past, most soil insects in the USA were effectively controlled by chlorinated hydrocarbon insecticides. However, nearly all widespread uses of these chemicals on wheat have been banned. Thus, in some areas cultural practices may be the only available control method.

9–2.4.1 Wireworms (Elateridae)

Many species of wireworms attack wheat throughout the world. The three most injurious to wheat in North America are: the wheat wireworm,

Agriotes mancus (Say); the prairie grain wireworm (*Ctenicera aeripennis destructor* (Brown); and the Great Basin wireworm, *C. pruinina* (Horn). The wheat wireworm is a pest of wheat in the northeastern and midwestern states and in eastern Canada. It is normally a grass feeder, living on roots in pastures and meadows, and prefers heavy, poorly-drained soils. The prairie grain wireworm is a serious pest of wheat in the northern Great Plains states and in western Canada. This species prefers well-drained light and medium soils of the open prairie. The Great Basin wireworm is an important pest of dryland wheat in the Pacific Northwest and western Canada. It originally fed on bunch grass, but became adapted to the summer-fallow practice in dryland areas.

Wireworms, the larval stage of click beetles, are elongate, cylindrical, and hard and wiry. They are shiny yellow or reddish brown and about 1 to 6 cm long, depending on species and age. The larva has a distinct head and three pairs of short stumpy legs. Click beetles are hard-shelled, brownish, grayish, or nearly black, with bodies tapering toward each end. Eggs are laid slightly below the surface of the soil and hatch in about 1 month. Young larvae move up and down in the soil in response to temperature and moisture. The duration of the life cycles of wireworms may be from 1 to 9 yr, most of which time is spent in the larval stage in the soil. Since generations overlap, all stages and all sizes of larvae may be found in the soil. The larvae pupate in the soil and change to the adult stage during late summer or fall.

Wireworms may attack wheat as soon as the crop is seeded. The larvae gnaw out the seeds, leaving only the seed coats. The greatest injury, however, is caused by their feeding on roots and underground portions of stems. This feeding usually kills the central shoot, and severely injured plants die. In addition to feeding damage, the wounds may also allow pathogens to invade the plants. Since the larvae prefer to feed on succulent tissue, plants that have tillered and are more mature often escape serious injury. Wireworm damage is first noticed in the fall or early spring as bare areas in fields. Damage is usually greatest in wheat fields that have been seeded after summer fallow or have been in grass for several years (Pfadt, 1985).

Wireworms are difficult to control, although cultural methods have been moderately successful in preventing damage. Since damage is mainly to seed and young plants, seeding and cultivation practices that hasten germination and increase plant vigor are beneficial. Clean cultivation practices during summer fallow also reduce wireworm populations. Deep plowing makes a highly favorable environment for wireworms.

9-2.4.2 False Wireworms (Tenebrionidae)

Several species of false wireworms are important pests of wheat in North America, primarily west of the Mississippi River and as far north as British Columbia and south to northern Mexico (Dahms, 1967). These insects inhabit large areas of the semidesert plains and perhaps originally

fed on seeds and roots of wild grasses before wheat became the preferred host. The species causing the greatest damage are *Eleodes hispilabris* (Say), *E. opacus* (Say), *E. tricostata* (Say), and *E. suturalis* (Say).

False wireworms, the larval stage of darkling beetles, closely resemble larvae of true wireworms. The larvae vary in color from yellowish brown to nearly black, are distinctly segmented, and may be up to 3 cm long. The adults are large, dull-black to reddish brown beetles. The wings are unusual in that they are fused together, making flight impossible. Adults are general feeders and seldom cause damage.

Damage to wheat by larvae is similar to that caused by true wireworms. The larvae feed on seed and young wheat sprouts and may even attack young plants by cutting the stems off below the soil surface. Injury is most severe during dry years or when wheat is seeded in soil too dry for rapid germination and emergence.

The life cycle and habits of the different species vary. Adults of *E. hispilabris* emerge in late summer and hibernate as adults. Eggs are laid singly in dry soil the following spring and early summer and hatch in about 15 days. The larvae may live from 1 to over 2 yr. The complete life cycle of the insect may require 1½ to 3½ yr, so two and sometimes three generations may be in the soil at one time. *Eleodes opacus*, *E. tricostata*, and *E. suturalis* have 1-yr life cycles, but some adults of *E. suturalis* may live 2 or 3 yr. These species overwinter as larvae and pupate in late spring. Adults emerge and become active early in the summer and lay their eggs in the soil. The young larvae feed on the seed, roots, and underground parts of stems of fall-seeded wheat. When the soil becomes cold, they burrow below the frost line and become inactive until spring.

Control measures for false wireworms are similar to those for true wireworms. Cultural practices that hasten growth and improve vigor of wheat are particularly important in reducing damage. Also, a 2-yr rotation of wheat with another crop and a clean cultivation summer fallow reduce injury.

9-2.4.3 White Grubs (Scarabaeidae)

White grub is the common name for larvae of a large group of polyphagous beetles. These insects have similar habits and feed on a wide range of cultivated and wild plants. Several species in the genus *Phyllophaga (Lachnosterna)* may cause serious injury to wheat in the USA, especially in the central and southern hard red winter wheat area. The adults are the well-known May or June beetles. The species vary in color from grayish to blackish brown and are about 2.5 cm long. They feed mainly on various weeds, shrubs, and crops. The larva is white-bluish and has six small legs. The head is brown and heavily chitinized. The body is soft, wrinkled, and crescent-shaped. The larva has three to four instars and is about 3 cm long when full grown.

Wheat may be damaged in the fall and spring. Wheat seeded early in the fall on grub-infested land is particularly susceptible to damage.

The most serious damage, however, occurs in the spring. The grubs feed on the roots, which usually results in sudden death of the plants. Where the roots are not completely destroyed, the plants may survive, but are stunted and fail to produce spikes.

Phyllophaga lanceolata (Say) is one of the most serious white grubs that attacks wheat. This species requires 2 yr to complete its life cycle. Eggs are laid singly in the soil and hatch in about 2 weeks into tiny grubs which may feed on decaying plant matter until roots of wheat plants are available. The young grubs feed just below the soil surface until early fall. They then migrate down into the soil, usually below the frost line, where they overwinter. As the soil warms in the spring, the larvae migrate upward and resume feeding on the roots until the plants are mature. Severe damage occurs in the fall of the second year when wheat is seeded early on the same land. The second downward migration takes place in the fall, and the grubs overwinter in a nearly full-grown stage. They pupate and change to adults in early spring. The adults feed and mate during early daylight hours and return to the soil during the day for protection and to lay eggs.

Preventive measures should be used for protecting wheat in areas known to be infested by white grubs. Cultural practices such as rotating wheat with legume crops, fallowing, and disking in the fall reduce damage. Fall damage may be reduced by seeding wheat sufficiently late so that roots are not available to the grubs before their winter migration begins. Several biotic agents such as insect parasites, pathogens, birds, and skunks are effective in reducing white grub populations.

9-2.4.4 Pale Western Cutworm (Noctuidae)

The pale western cutworm, *Agrotis orthogonia* Morrison, is a serious pest of wheat throughout most of the Great Plains of the USA and the Prairie region of western Canada. This cutworm, unlike others that attack wheat, is subterranean and feeds on the underground parts of stems. It thrives best in semiarid areas, and several successive dry springs may increase populations to outbreak proportions.

The pale western cutworm has one generation a year. The adult is a gray-colored moth with a wingspread of about 4 cm. The moths are active in early fall and lay 300 to 400 eggs each in loose dusty soil. Most of the eggs overwinter in the soil and hatch the following spring. The newly hatched larvae are about 1.5 mm long and almost colorless. They may feed for a short time on leaves of wheat plant, but soon enter the soil and feed thereafter on the plant from 1 to 2.5 cm below the soil surface. The larvae mature in late spring and are about 4 cm long and uniformly gray. They descend 7 to 13 cm in the soil and construct earthen cells for pupation. The adults emerge in early fall and search for suitable soil for laying eggs.

Winter wheat and spring barley are the favored hosts. Injury occurs in the spring about the time wheat begins to grow. Larvae sever the plants

just above the crown below the soil surface. Damage first appears as areas of wilting and dying plants. These damaged areas may enlarge rapidly and have the appearance of drought injury. When cutworm populations are high, entire fields may be destroyed in an extremely short time.

Since dry springs favor survival of the pale western cutworm, severity of infestations can be predicted (Hagan, 1974). Populations usually decline when 12 or more days from March to June receive at least 6 mm of rainfall per day, whereas when "wet days" total 10 or fewer, infestations are likely to be more injurious. Cultural practices such as plowing land to be summer-fallowed in the spring and delayed seeding of wheat in the fall will reduce damage.

9–2.5 Arthropod Vectors

In North America, BYDV and WSMV are the major wheat diseases caused by arthropod-transmitted viruses. Though WSMV can be mechanically transmitted, BYDV transmission is dependent solely on aphid vectors. BYDV is carried by about 20 species of aphids and infects nearly 100 species of Gramineae. With so many aphid vectors, BYDV is widely distributed in areas where wheat is grown. Several of the overwintering hosts of the aphids are also reservoirs for the virus. Even though there is obligate transmission, an outbreak of wheat aphids does not necessarily forecast a severe BYDV epidemic. Transmission is complicated by vector–virus–host and plant–environment interactions (Rochow, 1975). The virus is not transovarian, but persists in the aphid through progressive molts, so the aphid may remain viruliferous for life (Bruehl, 1961). Alate aphids are largely responsible for spreading BYDV, but predicting the dispersal of these aphids is difficult because they become airborne during windy weather. The aphids feed in the phloem, and the virus is translocated throughout the plant in about 24 hr (Carrigan et al., 1983). Visual symptoms of infection are variable and may be confounded, since feeding by some aphids causes discoloration of leaf tissue.

The complexities of BYDV transmission suggest that present control techniques for aphids may not control the disease. Insecticide treatment is recommended only when aphids have reached economic thresholds, so plants may already be inoculated with BYDV. Cultural practices such as the destruction of volunteer small grains or manipulation of the planting date are of limited value. Plant resistance to aphids causes the aphids to change feeding sites more frequently (Starks and Burton, 1977) and thus increases the disease incidence. Breeding wheats resistant to BYDV may be the best control approach. Sources of resistance (tolerance) to the virus are available (Qualset et al., 1977), but inheritance of resistance is complex (Cisar et al., 1982).

The aphids that transmit BYDV in wheat also are vectors of the pathogen in other cereals, but only the corn leaf aphid thrives on both maize and sorghum as well as small grains. In addition to BYDV, most wheat aphid species are also vectors of maize dwarf mosaic virus, a

serious problem in maize and sorghum but rare in wheat. The corn leaf aphid and *Brachycaudus helichrysi* Kalt transmit wheat mosaic streak virus in India and are the only known vectors of wheat yellow leaf virus in Japan. Aphids may interact with wheat pathogens in secondary ways. For example, aphid honeydew enhances infection of wheat leaves by *Cochliobolus sativus* Ito & Kurib and *Septoria nodorum* (Berk) (Fokkema et al., 1983).

Attempts in North America to transmit WSMV with species of mites such as the Banks grass mite have failed (Hill and Congdon, 1983). Thus, the wheat curl mite is the only known local vector of WSMV; however, it is a highly efficient one. The mite and virus have been associated together on about 50 species of Gramineae, mostly native grasses. Each has been found on a host where the other is absent, but nevertheless the association is close. Wheat, especially winter wheat, promotes the largest population of both. Only the immature stages of the mite acquire the virus, but it can persist and be transmitted by adults. The virus does not survive through the egg stage. Since virus transmission is dependent upon a single vector that moves relatively short distances, local control of the disease by controlling the vector can be practical. The destruction of volunteer small grains and host grasses in and around wheat fields will reduce both pests. The delay of wheat seeding until summer hosts such as maize and millet (*Panicum milaceum*) have become unpalatable food for the mite will reduce both the disease and mite in adjacent wheat. Even when prevention is not practiced, insecticides will effectively reduce both the vector and disease (Harvey et al., 1979).

The wheat curl mite also transmits the wheat spot mosaic organism (Nault and Styer, 1970). The pathogen has not yet been identified, and the disease is not considered serious. In Europe WSMV is transmitted by *Eriophyes tosichella* Keifer, a relative of the wheat curl mite. The grain rust mite, *Abacarus hystrix* (Nalepa), an occasional pest in the northern USA and adjacent parts of Canada, is a vector of Agropyron mosaic virus, a minor disease in wheat.

Compared to aphids and mites as vectors of wheat disease, leafhoppers and planthoppers transmit the greater number of pathogens, although the diseases incited are of lesser importance in North America. Wiese (1977) lists 46 wheat diseases resulting from viruses. Twelve of these are transmitted by at least 22 species of leafhoppers and 11 by 27 species of planthoppers. *Laodelphax striatelles* Fallen alone transmits viruses that cause three separate diseases in Europe and Asia. Only 4 of the 23 leafhopper-planthopper transmitted viral diseases of wheat have been reported in North America. These four are: American wheat striate mosaic, which is associated with the painted leafhopper, *Endria inimica* (Say), and *Elymana virescens* (F.) in the Dakotas and the Canadian Prairie Provinces; rice hoja blanca virus, carried by planthoppers *Sagota cabana* Crawford and *S. orizicola* Muir and restricted to the rice (*Oryza sativa* L.) -growing areas of the USA; oat blue dwarf virus, spread by leafhoppers

in the genus *Macrosteles*; and maize chlorotic dwarf spread by the black-faced leafhopper, *Graminella nigrifrons* (Forbes), but mainly on maize. Also, a mycoplasma-incited disease, aster yellows, is known to be carried only by the painted leafhopper and the aster leafhopper, *M. fascifrons* (Stål), in the northern USA and Canada. Additional viruses are probably transmitted by leafhoppers and planthoppers, but systemic toxins injected by the insects may resemble, mask, or interact with symptoms caused by viruses (Nuorteva, 1958).

The cereal leaf beetle, *Oulema melanopus* (L.), and the related *O. lichenis* (Voet.) are vectors of cocksfoot mottle virus in Europe. This is the only known case of a chewing insect transmitting a cereal virus, but cocksfoot mottle is also easy to transfer mechanically (Benigno and Brook, 1972).

9–3 CONTROL METHODS

9–3.1 Plant Resistance

The importance of plant resistance as a method of insect control has been recognized for many years. Plant resistance has a number of advantages over other insect control methods. It provides inherent protection at little additional cost. For crops of low cash value, plant resistance may be the only economical way to control certain pests. It is highly compatible with other control methods and often is used as the major component of integrated pest management programs. Because the effects of resistance on pest populations are specific, constant, and cumulative, cultivars with moderate or even low levels of resistance are highly useful.

Like other insect control methods, plant resistance has certain limitations and special problems are associated with its use. As pointed out by Jenkins (1981), these problems may affect both breeding for resistance and the permanence of resistant cultivars. The type of resistance expressed by plants is an important consideration in breeding for insect resistance. The mechanisms by which plants resist insects have been characterized as antibiosis, antixenosis, and tolerance (Painter, 1951; Kogan and Ortman, 1978). These mechanisms do not exclude each other, and the resistance expressed by a plant may be the result of one or more mechanisms. In some instances, a single mechanism of resistance may be sufficient to effect control, whereas in other cases it may be necessary to combine resistance mechanisms to obtain higher or more stable levels of resistance. However, one mechanism of resistance may be highly effective against the target pest but also increase plant susceptibility to other pest species.

The permanence of resistance is a major concern. The greatest threat to the permanence of resistance is the development of insect biotypes. Biotypes are more likely to develop when antibiosis is the mechanism of resistance since it places greater selection pressure on populations than

antixenosis or tolerance. Also, monogenic resistance is generally more vulnerable to biotypes than polygenic resistance (Gallun and Khush, 1980). Thus, when biotypes exist in the target species, strategies for breeding and management of resistant cultivars should be developed so that resistance to the pest can be maintained. Several strategies for managing resistant cultivars have been proposed for increasing the permanence of their resistance (Jenkins, 1981). Nearly all of these strategies are aimed at reducing selection pressure to delay the buildup of biotypes.

In North America, resistant cultivars of wheat are used as the primary method or in adjunct with other methods to control the Hessian fly, wheat stem sawfly, and cereal leaf beetle. The potential for expanded use of plant resistance has been demonstrated for other wheat pests, such as the greenbug and wheat curl mite. For these pests, sources of resistance are available, but resistant cultivars have not yet been developed.

9-3.1.1 Hessian Fly

Much success has been achieved in breeding wheats for resistance to the Hessian fly. During the period from 1950 to 1983, 60 Hessian fly-resistant cultivars were released in the USA. In 1979, about 8.4 million ha of wheat were seeded to 49 resistant cultivars in 36 states (Briggle et al., 1982). In areas where resistant cultivars have been grown for several years, losses by the Hessian fly have been reduced to $< 1\%$ (Maxwell et al., 1972).

Numerous sources of resistance to Hessian fly have been identified in wheat. The origin and genetics of resistance have been reviewed by Gallun (1977), Stebbins et al. (1983), and Hatchett and Gill (1983). Resistance is dominant, partially dominant, or recessive, and conditioned by single, duplicate, or multiple genetic factors. Thirteen major genes (designated *H1* through *H13*) have been identified. Other genetic factors for resistance include those derived from 'Marquillo' and 'Kawvale' wheats. The Marquillo-type resistance is complex. The genetic basis of resistance in Kawvale has not been determined. The primary mechanism of resistance controlled by these genes is antibiosis, i.e., first-instar larvae die after feeding on resistant plants. Most present-day resistant cultivars contain one or more major genes, *H3*, *H5*, or *H6*, or the Marquillo–Kawvale-type resistance.

The genetic interactions between wheat and the Hessian fly are highly specific; gene-for-gene relationships exist between resistance in the host and avirulence in the insect (Gallun and Khush, 1980). The ability of biotypes to infest resistant wheats is controlled by recessive genes. Eight biotypes of Hessian flies that differ in ability to infest wheats having specific resistance genes have been identified in the field (Gallun, 1977; Sosa, 1981). The strategy for management of resistance genes in breeding programs has been the sequential release of cultivars with different genes. Presently, three genes, *H3*, *H5*, and *H6*, have been utilized to increase the permanence of resistant cultivars. Although specific biotypes have

developed in some areas (Hatchett and Gallun, 1968; Hatchett, 1969; Sosa, 1981), populations have not reached damaging levels on most resistant cultivars. Other single genes resistant to the known biotypes have recently been identified (*H9* through *H13*) (Hatchett et al., 1981; Stebbins et al., 1982, 1983; Oellermann et al., 1983). The use of these genes in breeding programs should continue to enhance the permanence of resistance to the Hessian fly.

9-3.1.2 Wheat Stem Sawfly

Plant resistance has provided the best method for controlling the wheat stem sawfly. Eleven resistant cultivars have been released since the 1940s. In 1979, resistant cultivars were grown on about 0.4 million ha in the USA (Briggle et al., 1982). DePauw (1984) reported 0.4 million ha of resistant cultivars grown in Canada in 1983.

Resistance to wheat stem sawfly is associated primarily with stem solidness in wheat. The mechanism of sawfly resistance has been discussed by a number of workers (Holmes and Peterson, 1961, 1962; Wallace et al., 1973). In contrast to normal hollow stems of susceptible cultivars, solid stems of resistant cultivars appear to inhibit egg hatch and larval development. Stem solidness is a highly variable trait, and the degree of solidness influences the level of resistance (O'Keefe et al., 1960). Holmes and Peterson (1960) reported that solidness of the three lower internodes was more important for resistance expression than solidness of upper internodes.

The expression of stem solidness in wheat is affected by genetic and environmental factors. The genetics of the solid-stem trait in *Triticum* spp. has been reviewed by Wallace and McNeal (1966). Stem solidness may be conditioned by one or more dominant, recessive, or complementary genes. McKenzie (1965a, 1965b) showed that resistance of solid-stemmed 'CT 715' was conditioned by three genes that had unequal effects. Corresponding genetic factors and similar gene actions were expressed for stem solidness, an indication that stem solidness and resistance were closely associated. Several environmental factors have been shown to influence the degree of pith development and sawfly cutting in solid-stem cultivars. Platt et al. (1948) reported that stem solidness of common wheat was affected by variation in light, temperature, moisture supply, and spacing of plants. Holmes (1984) showed that resistance of solid-stem cultivars was significantly reduced at decreased light intensities.

The solid-stem character has often been associated with lower yields, and for this reason resistant cultivars have not been grown universally in sawfly-infested areas. The major source of stem-solidness has been 'Rescue', a spring wheat. McNeal et al. (1965) reported that yields of Rescue × 'Thatcher' (hollow-stem) derivatives were negatively correlated with increased stem solidness. However, Lebsock and Koch (1968) reported that stem solidness of Rescue × 'Conley' (hollow-stem) deriva-

tives was highly heritable and independent of agronomic traits. They concluded that although Rescue may be a poor combiner for yielding ability in some genetic backgrounds, selection for high-yielding solid-stemmed lines should be possible in sufficiently large populations. Quantitative methods have enabled breeders to select for solidness in the absence of sawfly and retain a broader-base population for selection of other agronomic characteristics (Wallace et al., 1973). Recent success has been demonstrated by the development and release of high-yielding sawfly-resistant cultivars, such as 'Lew' and 'Glenman' in the USA (McNeal and Berg, 1977; McNeal et al., 1984) and 'Leader' in Canada (DePauw et al., 1982). The breeding of these cultivars is evidence that stem solidness is not a limiting factor for improvement of yield.

9-3.1.3 Cereal Leaf Beetle

Breeding for resistance to the cereal leaf beetle began soon after its detection in Michigan in 1962. Detailed reviews of resistance in small grains to cereal leaf beetle have been published (Webster, 1977; Webster and Smith, 1983). Resistance of wheat to cereal leaf beetle is associated with leaf surface pubescence (Gallun et al., 1966; Schillinger and Gallun, 1968). The mechanism of resistance is primarily antixenosis, i.e., wheat having highly pubescent leaves are largely avoided by females for egg laying. Eggs that are occasionally deposited on pubescent leaves are more susceptible to desiccation. In addition, leaf pubescence interferes with larval feeding, especially that of newly hatched larvae. Wellso (1973) reported that larval development time was longer, larvae consumed less food, and fewer larvae survived on pubescent leaves than on glabrous leaves.

The deterrent effect of leaf pubescence on cereal leaf beetle oviposition and larval survival depends on both density and length of trichomes (Gallun et al., 1966; Hoxie et al., 1975). Webster et al. (1975) concluded that trichome densities of about 17 trichomes per mm^2 and lengths exceeding 250 μm were probably sufficient to deter oviposition when beetle populations were low. But high density (>35 trichomes per mm^2) and long trichomes may be more desirable when populations are high and few alternate hosts are available. The major source of pubescence has been 'CI 9321', a spring wheat introduction from the USSR. Ringlund and Everson (1968) found pubescence density was quantitatively inherited and gene action was mainly additive with partial dominance for dense pubescence. Leisle (1974) reported that density of pubescence in durum wheat 'PI 181000' was dominant in crosses with glabrous cultivars and that three genes conditioned the presence of pubescence in this wheat. Smith and Webster (1973) presented evidence that genes on chromosome 4A imparted high levels of resistance to oviposition and genes on chromosomes 5A, 2A, and 7B conferred low levels of resistance.

By the early 1980s, one cereal leaf beetle-resistant cultivar and 17 resistant wheat germplasms have been released (Webster and Smith, 1983).

'Downy', a soft red winter wheat (Roberts et al., 1981), has been grown primarily in cereal leaf beetle-infested areas of Indiana, Michigan, and Ohio (Briggle et al., 1982). In field tests, pubescent wheats have been shown to cause a reduction of over 96% in cereal leaf beetle oviposition (Gallun et al., 1973; Webster et al., 1973) and a reduction of 86% in larval densities (Casagrande and Haynes, 1975). Lampert et al. (1983) reported that the widespread introduction of pubescent wheats over a 5-yr period reduced the regional production of cereal leaf beetle adults and larvae. Pubescent wheats did not increase beetle populations in oat or susceptible wheat fields or affect parasitism by four parasite species (Webster and Smith, 1984).

The possibility that pubescent wheats may be more susceptible to other pests has been a major consideration. Roberts (1974) found no significant relationships between leaf pubescence and wheat leaf rust (*Puccinia recondita* f. sp. *tritici* Rob. ex Desm.), leaf blotch (*Septoria tritici* Rob. ex Desm.), and powdery mildew (*Erisyphe graminis* DC f. sp. *tritici* E. Marchal). Harvey and Martin (1980) found a direct association between wheat leaf pubescence and wheat streak mosaic virus and its vector, the wheat curl mite. Pubescent wheats had a higher incidence of virus and were more heavily infested by airborne wheat curl mites than glabrous wheats. They suggested that pubescent wheats probably should not be grown where wheat streak mosaic is a greater production hazard than the cereal leaf beetle.

9-3.1.4 Greenbug

Breeding for greenbug resistance in wheat began in the 1950s after resistance was found in 'Dickinson Sel. 28A', a hexaploid selection from a durum wheat (Dahms et al., 1955). Curtis et al. (1960) reported that the resistance mechanism of DS28A was tolerance to greenbug toxins, but Painter and Peters (1956) showed that greenbug reproduction on DS28A also was reduced. Several workers (see Gardenhire, 1980) reported that resistance of DS28A was conditioned primarily by a single recessive gene. During the 1960s, resistance of DS28A was overcome by biotype B greenbug (Wood, 1961), which became prevalent on wheat in the southern Great Plains before resistant cultivars were released. In 1968, biotype C became widespread, and not only damaged wheat, including DS28A, but also damaged commercial sorghum (Harvey and Hackerott, 1969; Wood, 1971).

Further sources of greenbug resistance were not available until Wood et al. (1974) identified tolerance and antibiosis to biotype C greenbugs in the 8× triticale 'Gaucho.' Resistance in Gaucho was conditioned by a single dominant gene derived from 'Insave F.A.' rye. Using x-ray techniques, Sebesta and Wood (1978) transferred resistance from Gaucho to the hexaploid wheat–rye translocation line 'Amigo'. Hollenhorst and Joppa (1983) verified a single dominant gene for resistance in Amigo and determined that the gene was located on chromosome 1A. Amigo germ-

plasm was used extensively in breeding programs until a new greenbug biotype (E) that severely damaged Amigo was detected (Porter et al., 1982). Kindler et al. (1984) showed that biotype E was widespread in the Great Plains.

Joppa et al. (1980) identified resistance in *T. tauschii* (PI 268210) and transferred the resistance to an amphiploid wheat. They found that the resistance (tolerance) was conditioned by a single dominant gene. The gene was located on chromosome 7D (Hollenhorst and Joppa, 1983). The hexaploid wheat germplasm 'Largo', having resistance derived from *T. tauschii*, was released in 1980 (Joppa and Williams, 1982). Further resistance studies by Porter et al. (1982) and Starks et al. (1983) showed that Largo also was resistant to biotype E. Harvey et al. (1980) identified greenbug resistance derived from *T. tauschii* var. *strangulata* and *typica* in several synthetic hexaploid wheats. Their results suggested that resistance of *strangulata* and *typica* was conditioned by different single dominant genes. Wheat germplasm 'KS8H640GB', resistant to greenbug biotype E and derived from *T. tauschii* var. *strangulata*, was released in 1982 (Martin et al., 1982). It is not known whether resistance derived from different *T. tauschii* sources carry the same or different genes. Tyler et al. (1985) reported resistance to biotype E in WSMV-resistant germplasm, with resistance apparently derived from *T. speltoides*. In triticale, resistance to biotype E was found in six plant introductions (Webster and Inayatullah, 1984).

9-3.1.5 Wheat Curl Mite

Sources of resistance to wheat curl mite have been identified in rye and wheat–*Elytrigia* lines. Martin et al. (1976) reported resistance to both wheat curl mite and wheat streak mosaic virus in wheat–*Elytrigia* substitution and translocation lines ('CI 15321', 'CI 15322'). They indicated that genes for mite resistance are either closely linked to genes controlling virus resistance, or both resistances are conditioned by the same genes. Harvey and Livers (1975) found several rye cultivars resistant to the mite, but the most promising resistance was identified in wheat–rye addition lines carrying chromosome 1R from rye. Further studies involving 1R chromosome substitution and translocation lines showed that the translocation line 'Salmon' was highly resistant to wheat curl mite, but susceptible to wheat streak mosaic virus (Martin et al., 1976). Resistance was inherited as a dominant trait, but the number of genes involved was not determined.

Wheat curl mite-resistant wheat germplasm 'KS80H4200' with resistance derived from Salmon was released in 1982 (Martin et al., 1983). The value of mite resistance to control wheat streak mosaic virus has been investigated by Martin et al. (1984). In field tests, wheat curl mite-resistant wheats reduced the incidence of the virus by an average of 58% when compared to mite-susceptible cultivars. Resistance to the mite appeared to be the result of antibiosis or antixenosis. These results indicate

that development of wheat cultivars resistant to wheat curl mite may provide an excellent means for reducing losses to wheat streak mosaic.

9–3.2 Cultural Control

Cultural controls are production practices that make the environment less favorable for the survival and reproduction of arthropod pests. Cultural methods have long been relied on to control insect pests of wheat. The major advantage of cultural control is that many of the methods can be applied as a part of normal production practices or with only slight modifications. The greatest disadvantage of cultural control is that the methods usually must be applied before damage is apparent and may require long-term planning. For cultural control practices to be effective, the methods must be properly coordinated with the life history and habits of the pests and applied during the most vulnerable stages of their life cycle. Cultural controls are aimed at preventing damage rather than eliminating existing infestations. They are most effective when used over large areas and in conjunction with other control methods.

Wheat cultural practices that have proved effective in reducing insect damage include promotion of vigorous plants and stands, crop rotation, clean culture, tillage, and timing of seeding and harvesting (Pfadt, 1985). Some cultural methods may reduce populations of one insect, but increase survival and damage by another species. In most cases, however, cultural control practices are important in protecting the crop and should be considered in any integrated control program. Sometimes a slight population reduction of pests delays build-up to damaging levels.

Since wheat can tolerate a moderate amount of insect injury with little loss in yield and quality, agronomic practices that promote vigorous growth of plants usually aid in reducing damage. Vigorous stands are better able to withstand infestations of the Hessian fly, aphids, wheat jointworm, wheat stem sawflies, and wireworms. Also some insects such as the Hessian fly, sawfly, and chinch bug prefer to lay their eggs or congregate in thin stands. Seeding practices that hasten germination and stimulate tillering give young plants a better chance to outgrow insect attack or recover from injury.

Rotation of wheat with other crops is most effective against pests that have restricted host ranges or limited migration habits. Crop rotations that avoid continuous wheat or other small grains reduce populations of sawfly, Hessian fly, wheat strawworm, white grubs, false wireworm, and winter grain mite.

Survival of many wheat pests depends on adequate food and protection from the time of harvest until the new crop is seeded. Thus cultural practices that destroy crop residues, volunteer plants, and alternate hosts aid greatly in reducing damage to the next crop. Clean cultivation reduces damage by the Hessian fly, wheat curl mite, false wireworm, wheat strawworm, stem sawfly, and grasshoppers, but may promote erosion.

Soil tillage has been recognized for many years as a valuable method for controlling insects. Tillage not only destroys host plants, but may bury some insects so deeply that few survive. Plowing under infested stubble soon after harvest reduces infestations of Hessian fly, wheat stem sawfly, and other insects that remain in crop residue. Plowing also destroys many grasshopper eggs and soil insects by exposing them to natural enemies and unfavorable weather. In some areas, tillage may increase soil erosion or interfere with water management or other cropping practices.

Timing of wheat seeding and harvesting may have an important influence on insect infestation and damage. Control of some pests is achieved by seeding the crop when the pest is not present or is least abundant. Delayed seeding of winter wheat in the fall reduces infestations by the Hessian fly, wheat stem maggot, grasshopper, white grubs, and wheat curl mite. In spring wheat areas, early seeding is an important factor in reducing damage by the Hessian fly and frit fly. Harvesting the crop early before maximum stem breakage occurs can reduce damage by the Hessian fly and wheat stem sawfly.

9–3.3 Chemical Control

Insecticides remain the main line of defense against some pests and are the only practical means of control in outbreaks of pests such as greenbugs, armyworms, and cutworms. Properly used, insecticides will rapidly prevent economic damage. The use of aircraft makes it possible for large area of wheat to be treated quickly and efficiently and without the mechanical damage caused by ground equipment. In 1976, 6 358 500 ha of wheat in the USA were treated with 1 407 400 kg of actual insecticide, while in 1982, 2 916 000 ha were treated with 1 089 600 kg of actual insecticide. Parathion was applied on approximately 40% of the treated hectares both years (Delvo and Hanthorn, 1983). The greater usage in 1976 was undoubtedly caused by the greenbug outbreak in the Great Plains.

The use of insecticides on wheat should be reserved for emergency, outbreak situations when natural enemies or cultural practices are not effective and when resistant cultivars are not available. With wheat, it is expensive and unnecessary to use insecticides as prophylactic treatments as is often done with high-unit-value crops. Often, only one properly timed application of an insecticide is needed to control most pests of wheat.

The improper use of an insecticide may result in the resurgence of both the target species and other pests because of the destruction of beneficial insects. The hazards of pesticide residues must also be considered, especially when applications are made on wheat used as a forage crop and also on stored grain (Hormann, 1980). In 1981, about 105 300 ha of wheat in Montana, South Dakota, Wyoming, and Colorado were sprayed by air to control the pale western cutworm and the army cutworm.

However, game birds were contaminated with residue levels up to four times the limit considered safe. In addition, the 20 million migrating waterfowl traversing the area extended the contamination to the 17 states of the Western Flyway (Metcalf and Luckmann, 1982). Many of the insecticides used on wheat are highly toxic, not only to insects but also to humans. Thus, proper safety precautions are a necessity when using insecticides.

One of the most important reasons for the judicious use of insecticides is the resistance problem. Over 260 species of arthropods have been reported to be resistant to commonly used insecticides (Georghiou and Mellon, 1983). So far, the only important insecticide-resistant pests of wheat are the greenbug and the Banks grass mite (Ward et al., 1972), but insecticide-resistant wheat pests may become a serious problem, because there are only 11 different pesticides presently registered for use on wheat. Likely, few new insecticides for use on wheat will be available because of the low demand and high costs of production and testing of potential chemicals.

Insect growth regulators are selective chemicals that disrupt the action of the insects' hormone systems, which in turn affect growth, metamorphosis, and reproduction. Their best potential use against wheat pests appears to be in preventing immature insects from developing into adults. Chemosterilants are chemicals that cause reproductive sterility; however. they are all highly mutagenic and carcinogenic to humans, so their use is doubtful (Metcalf and Metcalf, 1982). Semiochemicals are chemical substances that deliver behavioral messages, and pheromones are semiochemicals used in intraspecific communication (i.e., between individuals of a single species). The pheromone group is among the most ecologically selective pest management agents now being investigated (Klassen et al., 1982). Pheromones have been identified for some pests of wheat, but they are currently more useful in monitoring than in controlling insects. Research on chemical repellents for foliage-feeding insects has not progressed as far as chemical attractants, since they appear to offer few advantages and may produce the same environmental hazard as conventional insecticides.

9–3.4 Biological Control

Just as wheat is an abundant food source for arthropod pests, the pests of wheat provide a food source for biological enemies. These enemies include other arthropods and nematodes acting as parasites and predators, pathogenic microbes, and predacious vertebrates. Pests like leaf-feeding sawflies in the genus *Pachynematus* (Painter et al., 1954) fluctuate little from year to year, presumably because parasites stabilize the population within narrow limits. Other pests periodically gain reproductive advantages over enemies, and outbreaks occur. But even outbreaks may suddenly collapse because of the interaction of complex biotic and abiotic factors.

Most parasites and predators lag behind their hosts in seasonal development, and some do not have life cycles that are synchronized with those of wheat pests. As an example, *Lysiphlebus testaceipes* does not become active until the temperature exceeds 15 °C, but the greenbug starts reproduction at about 10 °C. A native parasite is efficient against the wheat stem sawfly in grasses, but its development is not synchronized with pest's activity on wheat (Wallace and McNeal, 1966). Some natural enemies of wheat pests have wide host ranges and may choose other available hosts. Parasites and predators also have their enemies, and these may depress beneficial populations at the time pests are increasing. Beneficial insect numbers are greatly reduced after most insecticidal treatments of wheat. This, however, is not a widespread problem, since only about 7% of the wheat hectarage is treated per year.

In the USA, exotic beneficial insects have systematically been released to combat introduced wheat pests, especially the ones from Asia and Europe. Most of these attempts have failed, but the successes have been important. *Pediobius metallicus* (Nees), a parasite attacking the Hessian fly, has become widely established (Clausen, 1956). The introduced European wheat stem sawfly parasite, *Collyria coxator* (Villers), is well established in the eastern USA, and the pest has declined (Streams and Cole, 1965). Introduced egg and larval parasites of the cereal leaf beetle have become effective in the north-central USA (Haynes and Gage, 1981). Several parasites and predators of cereal aphids have been introduced since the 1950s, but none at present have become widely established (Rogers et al., 1972b).

Inundative releases of beneficial insects to control cereal pests offer little promise with current technology (Hagan, 1962). Augmentation of existing beneficial insect populations is perhaps more feasible, but there is little evidence that the procedures will be economical (Starks et al., 1976). Salticid spiders are often numerous prey on pests, live a relatively long time, and can be artificially reared (Horner and Starks, 1972). However, their slow reproductive rates probably destine them to secondary roles as predators.

Among the vertebrate predators that feed on large-sized pests of wheat, birds are probably the most visible. The story of gulls eliminating infestations of Mormon crickets is often told. Insectivorous birds effectively reduce populations of army cutworm (Burton et al., 1980). Reptiles and small mammals also include wheat pests in their diets. The management of vertebrate predators remains largely unattempted.

Disease organisms are thought to be important factors regulating pale western cutworms and chinch bugs (Wilde, 1981). In fact, no pest species is thought to be free of pathogens. The incidence of infection is often high during pest outbreaks, but damage to wheat may have already occurred. It is now possible to use microbial insecticides even on crops planted over large areas. Some of these microbials, such as *Bacillus thuringiensis* Berliner and *Nosema locustae* Channing, have a fairly broad pathogenic spectrum.

REFERENCES

Aldrich, J.M. 1920. European frit fly in North America. J. Agric. Res. 18:451–474.

Allen, W.M., and R.H. Painter. 1937. Observations on the biology of the wheat stem maggot in Kansas. J. Agric. Res. 55:215–238.

Arriaga, H.O., H.O. Chidichimo, and L.B. Almaraz. 1983. Evaluación de resistencia a pulgón verde *Schizaphis graminum* (Rond.) en trigo. Rev. Fac. Agron., Univ. Nac. La Plata 56:53–60.

Ba-Angood, S.A., and R.K. Stewart. 1980a. The effect of timing of insecticide application on cereal aphid infestation and damage to barley in southwestern Quebec. Ann. Soc. Entomol. Que. 25:72–76.

----, and ----. 1980b. Effect of cereal aphid infestation on grain yield and percentage protein of barley, wheat, and oats in southwestern Quebec. Can. Entomol. 112:681–686.

Bakker, T., and A.G. Robinson. 1975. Movements of English grain aphids on barley plants. Manit. Entomol. 9:9–12.

Barbulescu, A. 1980. Evolution of *Schizaphis graminum* (Rond.) species. Appearance forms within its biological cycle. An. Inst. Cercet. Cereale Plante Teh. Fundulea 45:391–397.

Barnes, H.F. 1956. Gall midges of economic importance. p. 57–82. *In* H.F. Barnes (ed.) Gall midges of cereal crops, Vol. VII. Crosby Lockwood and Sons, London.

Battenfield, S.L., S.G. Wellso, and D.L. Haynes. 1982. Bibliography of the cereal leaf beetle, *Oulema melanopis* (L.) (Coleoptera: Chrysomelidae). Bull. Entomol. Soc. Am. 28:291–301.

Bauernfeind, R.J. 1983. Biotype E greenbug (Homoptera: Aphididae) control on wheat with insecticide sprays at low temperature. J. Econ. Entomol. 76:570–572.

Benigno, D.A., and J.A. Brook. 1972. Infection of cereals by cocksfoot mottle and Phleum mottle virus. Ann. Appl. Biol. 72:43–52.

Bonnemaison, L. 1980. Principal animal pests. p. 59–68. *In* E. Hafliger (ed.) Wheat. Documenta Ciba-Geigy. Tech. Monogr. Ciba-Geigy, Basel, Switzerland.

Branson, T.F. 1971. Resistance of spring wheat to the wheat stem maggot. J. Econ. Entomol. 64:941–945.

Briggle, L.W., S.L. Strauss, D.E. Hamilton, and G.H. Howse. 1982. Distribution of the varieties and classes of wheat in the United States in 1979. USDA-ARS Stat. Bull. 676. U.S. Government Printing Office, Washington, DC.

Bruehl, G.W. 1961. Barley yellow dwarf. Am. Phytopathol. Soc. Monogr. 1. American Phytopathological Society, St. Paul.

Burton, R.L., and E.G. Krenzer, Jr. 1985. Reduction of greenbug (Homoptera: Aphididae) populations by surface residues in wheat tillage studies. J. Econ. Entomol. 78:390–394.

----, K.J. Starks, and D.C. Peters. 1980. The army cutworm. Okla. Agric. Exp. Stn. Bull. B-749.

Carrigan, L.L., H.W. Ohm, and J.E. Foster. 1983. Barley yellow dwarf virus translocation in wheat and oats. Crop Sci. 23:611–612.

Cartwright, W.B., and E.T. Jones. 1953. The Hessian fly and how losses from it can be avoided. USDA Farmers' Bull. 1627. U.S. Government Printing Office, Washington, DC.

Casagrande, R.A., and D.L. Haynes. 1975. Impact of pubescent wheat on the population dynamics of the cereal leaf beetle. Environ. Entomol. 5:153–159.

Cisar, G., C.M. Brown, and H. Jedinski. 1982. Diallel analysis for tolerance in winter wheat to the barley yellow dwarf virus. Crop Sci. 22:328–333.

Clausen, C.P. 1956. Biological control of insect pests in the continental U.S. USDA Tech. Bull. 1139. U.S. Government Printing Office, Washington, DC.

Coggin, D.L., and G.P. Dively. 1982. Sequential sampling plan for the armyworm in Maryland small grains. Environ. Entomol. 11:169–172.

Cuperus, G., and R.A. Johnston. 1984. Wheat production and pest management in Oklahoma. Okla. State Univ. Coop. Ext. Serv. Circ. E-831.

Curtis, B.C., A.M. Schlehuber, and E.A. Wood, Jr. 1960. Genetics of greenbug, *Toxoptera graminum* (Rond.), resistance in two strains of common wheat. Agron. J. 52:599–602.

Dahms, R.G. 1967. Insects attacking wheat. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:411–443.

----, R.V. Connin, and W.D. Guthrie. 1954. Grasses as hosts of the greenbug. J. Econ. Entomol. 40:1151–1152.

----, T.H. Johnston, A.M. Schlehuber, and E.A. Wood, Jr. 1955. Reaction of small-grain varieties and hybrids to greenbug attack. Okla. Agric. Exp. Stn. Tech. Bull. T-55.

Delvo, H., and M. Hanthorn. 1983. Pesticides. p. 4–13. *In* Inputs outlook and situation. USDA Econ. Res. Serv. IOS-2. U.S. Government Printing Office, Washington, DC.

DePauw, R.M. 1984. Acreage sown to cultivars with resistance to wheat stem sawfly and 'Leader,' a new sawfly-resistant wheat. Annu. Plant Resist. Insects Newsl. 10:54–55.

----, D.S. McBean, T.F. Townley-Smith, J.M. Clark, T.N. McCaig, and S.R. Buzinski. 1982. Registration of Leader wheat. Crop Sci. 22:1265–1266.

DePew, L.J. 1968. Further evaluation of acaricides for brown wheat mite control on winter wheat in Kansas. J. Econ. Entomol. 61:1171–1174.

----. 1982. Chemical control of greenbugs in winter wheat under cool conditions in Kansas. J. Kans. Entomol. Soc. 55:562.

Fokkema, N.J., I. Riphagan, R.J. Poot, and C. de Jong. 1983. Aphid honeydew a potential stimulant of *Cochliobolus sativus* and *Septoria nodorum* and the competitive role of saprophytic mycoflora. Trans. Br. Mycol. Soc. 81:355–364.

Gage, S.H., and M.K. Mukerji. 1978. Crop losses associated with grasshoppers in relation to economics of crop production. J. Econ. Entomol. 71:487–498.

Gair, R., and F.E. Maskell. 1982. Wheat bulb fly. Great Britain Ministry of Agriculture, Fisheries and Food. Advisory Leaflet 177.

Gallun, R.L. 1977. Genetic basis of Hessian fly epidemics. Ann. New York Acad. Sci. 287:223–229.

----, R.T. Everly, and W.T. Yamazaki. 1967. Yield and milling quality of Monon wheat damaged by feeding of cereal leaf beetle. J. Econ. Entomol. 60:365–369.

----, and G.S. Khush. 1980. Genetic factors affecting expression and stability of resistance. p. 63–85. *In* F.G. Maxwell and P.R. Jennings (ed.) Breeding plants resistant to insects. John Wiley and Sons, New York.

----, J.J. Roberts, R.E. Finney, and F.L. Patterson. 1973. Leaf pubescence of field grown wheat: A deterrent to oviposition by the cereal leaf beetle. J. Environ. Qual. 2:333–334.

----, R. Ruppel, and E.H. Everson. 1966. Resistance of small grains to the cereal leaf beetle. J. Econ. Entomol. 59:827–829.

Gardenhire, J.H. 1980. Breeding for greenbug *Schizaphis graminum* (Rond.) resistance in wheat and other small grains. p. 237–244. *In* M.K. Harris (ed.) Biology and breeding for resistance to arthropods and pathogens in agricultural plants. Proc. Int. Shortcourse in Host Plant Resistance, College Station, TX. 22 July-4 Aug. 1979. MP-1451. Texas A&M University, College Station.

Georghiou, G.P., and R.B. Mellon. 1983. Pesticide resistance in time and space. p. 1–46. *In* G.P. Georghiou and T. Saito (ed.) Pest resistance to pesticides. Plenum Press, New York.

Gilchrist, L.I., R. Rodriguez, and P.A. Burnett. 1984. The extent of Freestate streak and *Diuraphis noxia* in Mexico. p. 157–163. *In* Barley Yellow Dwarf; Proc. of the Workshop. Centro Internacional par Mejoramiento de Maíz y Trigo (CIMMYT), Mexico.

Grewal, T.S., and S.S. Bains. 1975. The role of abiotic and biotic factors in the population build-up of wheat aphids and the extent of loss caused by them. Ind. J. Ecol. 2:139–145.

Hagan, A.F. 1974. Pale western cutworm in wheat. Nebr. Ext. Leaflet C-12.

Hagan, K.S. 1962. Biology and ecology of predaceous *Coccinellidae*. Ann. Rev. Entomol. 7:289–326.

Harvey, T.L., and H.L. Hackerott. 1969. Recognition of a greenbug biotype injurious to sorghum. J. Econ. Entomol. 62:776–779.

----, ----, and T.L. Martin. 1982. Dispersal of alate biotype C greenbugs in Kansas. J. Econ. Entomol. 75:36–39.

----, and R.W. Livers. 1975. Resistance to wheat curl mite, *Aceria tulipae* Keifer, in rye and wheat–rye addition lines. Environ. Entomol. 4:523–526.

----, and T.J. Martin. 1980. Effect of wheat pubescence on infestations of wheat curl mite and incidence of wheat streak mosaic. J. Econ. Entomol. 73:225–227.

----, ----, and R.W. Livers. 1980. Resistance to biotype C greenbug in synthetic hexaploid wheats derived from *Triticum tauschii*. J. Econ. Entomol. 73:387–389.

----, ----, and C.A. Thompson. 1979. Controlling wheat curl mite and wheat streak mosaic virus with systemic insecticide. J. Econ. Entomol. 72:854–855.

Hatchett, J.H. 1969. Race E, sixth race of Hessian fly, *Mayetiola destructor*, discovered in Georgia wheat fields. Ann. Entomol. Soc. Am. 62:667–678.

----, and R.L. Gallun. 1968. Frequency of Hessian fly, *Mayetiola destructor*, races in field populations. Ann. Entomol. Soc. Am. 61:1446–1449.

----, and B.S. Gill. 1983. Expression and genetics of resistance to Hessian fly in *Triticum tauschii* (Coss.) Schmal. p. 807–811. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Kyoto University, Kyoto.

----, T.J. Martin, and R.W. Livers. 1981. Expression and inheritance of resistance to Hessian fly in synthetic hexaploid wheats derived from *Triticum tauschii* (Coss.) Schmal. Crop Sci. 21:731–734.

Haynes, D.L., and S.H. Gage. 1981. The cereal leaf beetle in North America. Ann. Rev. Entomol. 26:259–287.

Henderson, I.F., and J.N. Perry. 1978. Some factors affecting the build-up of cereal aphid infestations in winter wheat. Ann. Appl. Biol. 89:177–183.

Hight, S.C., R.D. Eikenbary, R.J. Miller, and K.J. Starks. 1972. The greenbug and *Lysiphlebus testaceipes*. Environ. Entomol. 1:205–209.

Hill, J.P., and B.D. Congdon. 1983. Attempts to transmit wheat streak mosaic virus using Banks grass mite. Phytopathology 72:963.

Hollenborst, M.M., and L.R. Joppa. 1983. Chromosomal location of genes for resistance to greenbug in 'Largo' and 'Amigo' wheats. Crop Sci. 23:91–93.

Holmes, N.D. 1984. The effect of light on the resistance of hard red spring wheats to the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae). Can. Entomol. 116:667–684.

----, and L.K. Peterson. 1960. The influence of the host on oviposition by the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). Can. J. Plant Sci. 40:29–46.

----, and ----. 1961. Resistance of spring wheats to the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). I. Resistance to the egg. Can. Entomol. 93:250–260.

----, and ----. 1962. Resistance of spring wheats to the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). II. Resistance to the larvae. Can. Entomol. 94:348–364.

Hormann, W.D. 1980. Pesticide residues in wheat. p. 91–95. *In* E. Hafliger (ed.) Wheat. Documenta Ciba-Geigy. Tech. Monogr. Ciba-Geigy, Basel, Switzerland.

Horner, N.V., and K.J. Starks. 1972. Bionomics of the jumping spider *Metaphidippus galathea*. Ann. Entomol. Soc. Am. 65:602–607.

Hoxie, R.P., S.G. Wellso, and J.A. Webster. 1975. Cereal leaf beetle response to wheat trichome length and density. Environ. Entomol. 4:365–370.

Jabbar, A., and M. Ahmed. 1980. Feeding effects of *Zyginidia quyumi* (Ahmed) on foliage of wheat and maize in Pakistan. Pak. J. Sci. Res. 32:21–24.

Jacobson, L.A. 1965. Damage to wheat by Say stink bug, *Chlorochroa sayi* Stål. Can. J. Plant Sci. 45:413–417.

Jenkins, J.N. 1981. Breeding for insect resistance. p. 291–308. *In* Plant breeding II. Iowa State University Press, Ames.

Joppa, L.R., R.G. Timian, and N.D. Williams. 1980. Inheritance of resistance to greenbug toxicity in an amphiploid of *Triticum turgidum/T. tauschii*. Crop Sci. 20:343–344.

----, and N.D. Williams. 1982. Registration of Largo, a greenbug resistant hexaploid wheat. Crop Sci. 22:901–902.

Kieckhefer, R.W. 1975. Field populations of cereal aphids in South Dakota spring grains. J. Econ. Entomol. 68:161–164.

----, W.F. Lytle, and W. Spuhler. 1974. Spring movement of cereal aphids into South Dakota. Environ. Entomol. 3:347–350.

Kindler, S.D., S.M. Spomer, T.L. Harvey, R.L. Burton, and K.J. Starks. 1984. Status of biotype E greenbugs (Homoptera: Aphididae) in Kansas, Nebraska, Oklahoma, and Northern Texas during 1980–1981. J. Kans. Entomol. Soc. 57:155–158.

Klassen, W., R.L. Ridgway, and M. Inscoe. 1982. Chemical attractants in integrated pest management programs. p. 13–130. *In* Insect suppression with controlled release pheromone systems, Vol. 1. CRC Press, Boca Raton, FL.

Kogan, M., and E.F. Ortman. 1978. Antixenosis: A new term proposed to define Painter's "nonpreference" modality of resistance. Bull. Entomol. Soc. Am. 24:175–176.

Kring, T.J., and F.E. Gilstrap. 1983. Within-field distribution of greenbugs (Homoptera: Aphididae) and its parasitoids in Texas winter wheat. J. Econ. Entomol. 76:57–62.

Lampert, E.P., D.L. Haynes, A.J. Sawyer, D.P. Jokinen, S.G. Wellso, R.L. Gallun, and J.J. Roberts. 1983. Effects of regional releases of resistant wheats on the population dynamics of the cereal leaf beetle (Coleoptera: Chrysomelidae). Ann. Entomol. Soc. Am. 76:972–980.

Lara, F.M., A.J.B. Galli, and A.C. Busoli. 1983. Tipos de resistencia de *Sorghum bicolor* (L.) Moench a *Schizaphis graminum* (Rondani 1852) (Homoptera: Aphididae). Cientifica 9:273–280.

Lebsock, K.L., and E.J. Koch. 1968. Variation of stem-solidness in wheat. Crop Sci. 8:225–230.

Leisle, D. 1974. Genetics of leaf pubescence in durum wheat. Crop Sci. 14:173–174.

Lilly, A.H.R. 1947. Investigations on the gout fly (*Chlorops pumilionis* Bjerk.) in Devon and Cornwall. Ann. Appl. Biol. 34:551–561.

Lowe, H.J.B. 1983. Some observations on susceptibility and resistance of winter wheat to the aphid *Sitobion avenae* (F.) in Britain. Crop Protect. 1:431–440.

Markkula, M., and K. Roukka. 1972. Resistance of cereals to the aphids *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (F.) and fecundity of these aphids on Gramineae, Cyperaceae, and Juncaceae. Ann. Agric. Fenn. 11:417–423.

Martin, T.J., and T.L. Harvey. 1982. Cultivar response to wheat strawworm. Crop Sci. 22:1233–1235.

----, ----, C.G. Bender, and D.L. Seifers. 1984. Control of wheat streak mosaic virus with vector resistance in wheat. Phytopathology 74:963–964.

----, ----, ----, ----, and J.H. Hatchett. 1983. Wheat curl mite resistant wheat germplasm. Crop Sci. 23:809.

----, ----, and J.H. Hatchett. 1982. Registration of greenbug and Hessian fly resistant wheat germplasm. Crop Sci. 22:1089.

----, ----, and R.W. Livers. 1976. Resistance to wheat streak mosaic virus and its vector, *Aceria tulipae*. Phytopathology 66:346–350.

Maxwell, F.G., J.N. Jenkins, and W.L. Parrott. 1972. Resistance of plants to insects. Adv. Agron. 24:187–251.

Mayo, ZB, Jr., and K.J. Starks. 1974. Temperature influences on alary polymorphism in *Schizaphis graminum*. Ann. Entomol. Soc. Am. 67:421–423.

McAlpine, J.F., and C. Slight. 1981. The wheat bulb fly, *Delia coarctata*, in North America (Diptera: Anthomyiidae). Can. Entomol. 113:615–621.

McKenzie, H. 1965a. Inheritance of sawfly reaction and stem solidness in spring wheat crosses: Sawfly reaction. Can. J. Plant Sci. 45:583–589.

----. 1965b. Inheritance of sawfly reaction and stem solidness in spring wheat crosses: Stem solidness. Can. J. Plant Sci. 45:591–600.

McNeal, F.H., W.L. Alexander, C.F. McGuire, J.W. Bergman, G.R. Carlson, A.L. Dubbs, G.D. Kushnak, G.F. Stallknecht, V.R. Stewart, E.L. Sharp, and B.K. Sally. 1984. Glenman wheat. Mont. Agric. Exp. Stn. Bull. 1497.

----, and M.A. Berg. 1977. Registration of Lew wheat. Crop Sci. 17:674.

----, C.A. Watson, M.A. Berg, and L.E. Wallace. 1965. Relation of stem solidness to yield and lignin content in wheat selections. Agron. J. 57:20–21.

McPherson, R.M. 1983. Damage potential of cereal leaf beetles (Coleoptera: Chrysomelidae) in Virginia small grains and corn. J. Econ. Entomol. 76:1285–1287.

Metcalf, R.L., and W.H. Luckmann. 1982. Introduction to insect pest management. 2nd ed. John Wiley and Sons, New York.

----, and R.A. Metcalf. 1982. Attractants, repellents, and genetic control in pest management. p. 275–306. *In* R.L. Metcalf and W.H. Luckman (ed.) Introduction to insect pest management. 2nd ed. John Wiley and Sons, New York.

Mills, H.B. 1939. Montana insect pests for 1937 and 1938. Mont. Agric. Exp. Stn. Bull. 366.

Nault, L.R., and W.E. Styer. 1970. Transmission of an eriophyid-borne wheat pathogen by *Aceria tulipae*. Phytopathology 60:1616–1618.

Nuorteva, P. 1958. On the nature of the injury to plants caused by *Calligypona pellucida* (F.) (Hom. areopidae). Ann. Entomol. Fenn. 24:49–59.

Oellermann, C.M., F.L. Patterson, and R.L. Gallun. 1983. Inheritance of resistance in 'Luso' wheat to Hessian fly. Crop Sci. 23:221–224.

O'Keefe, L.E., J.A. Callenbach, and K.L. Lebsock. 1960. Effect of culm solidness on the survival of the wheat stem sawfly. J. Econ. Entomol. 53:244–246.

Onsager, J.A., N.E. Rees, J.E. Henry, and R.N. Foster. 1981. Integration of bait formulations of *Nosema locustae* and carbaryl for control of rangeland grasshoppers. J. Econ. Entomol. 74:183–187.

Osborn, H. 1932. Leafhoppers injurious to cereal and forage crops. USDA Circ. 241. U.S. Government Printing Office, Washington, DC.

Painter, R.H. 1951. Insect resistance in crop plants. Macmillan Co., New York.

----, H.R. Bryson, and D.A. Wilbur. 1954. Insects that attack wheat in Kansas. Kans. Agric. Exp. Stn. Bull. 367.

----, and D.C. Peters. 1956. Screening wheat varieties and hybrids for resistance to the greenbug. J. Econ. Entomol. 49:546–548.

Palival, Y.C. 1982. Role of perennial grasses, winter wheat, and aphid vectors in the disease cycle and epidemiology of barley yellow dwarf. Can. J. Plant Pathol. 4:367–374.

Parker, J.R. 1954. Grasshoppers—A new look at an ancient enemy. USDA Farmers' Bull. 2064. U.S. Government Printing Office, Washington, DC.

Paulian, F., and C. Popov. 1980. Sunn pest or cereal bug. p. 69–74. *In* E. Hafliger (ed.) Wheat. Documenta Giba-Geigy. Tech. Monogr. Ciba-Geigy, Basel, Switzerland.

Pfadt, R.E. 1985. Insect pests of small grains. p. 241–281. *In* R.E. Pfadt (ed.) Fundamentals of applied entomology. Macmillan Co., New York.

Phillips, W.J., and F.W. Poos. 1940. The wheat jointworm and its control. USDA Farmers' Bull. 1006. U.S. Government Printing Office, Washington, DC.

----, and ----. 1953. The wheat strawworm and its control. USDA Farmers' Bull. 1323. U.S. Government Printing Office, Washington, DC.

Pike, K.S., and A.L. Antonelli. 1981. Hessian fly in Washington. Wash. State Univ. Agric. Res. Ctr. Bull. 0909.

Platt, A.W., C.W. Farstad, and J.A. Callenbach. 1948. The reaction of Rescue wheat to sawfly damage. Sci. Agric. 28:154–161.

Porter, K.B., G.L. Peterson, and O. Vise. 1982. A new greenbug biotype. Crop Sci. 22:847–850.

Qualset, C.O., P.E. McGuire, H.E. Vogt, and M.A. Topcu. 1977. Ethiopia as a source of resistance to the barley yellow dwarf virus in tetraploid wheat. Crop Sci. 17:527–529.

Rademacher, V.B. 1967. Untersuchungen über die tatsachlichen Ertragsschaden bei Befall

von Winterweizen und Sommergerste durch die beiden Getreidenhähnchen (*Lema cyanella* L. und *L. melanopus* L.) sowie durch die Getreidehalmwespe (*Cephas pygmaeus* L.). Z. Pflanzenkrk. Pflanzenschutz. 74:311–316.

Ratcliffe, R.H., and J.J. Murray. 1983. Selection for greenbug (Homoptera: Aphididae) resistance in Kentucky bluegrass cultivars. J. Econ. Entomol. 76:1221–1224.

Rautapää, J. 1966. The effect of the English grain aphid *Macrosiphum avenae* (F.) (Hom., Aphididae) on the yield and quality of wheat. Ann. Agric. Fenn. 5:334–341.

Ringlund, K., and E.H. Everson. 1968. Leaf pubescence in common wheat, *Triticum aestivum* L., and resistance to the cereal leaf beetle, *Oulema melanopus* (L.). Crop Sci. 8:705–710.

Roberts, J.J. 1974. Leaf pubescence of soft red winter wheat: its inheritance and association with important insect pests, diseases, and agronomic characters. Ph.D. diss. Purdue Univ., West Lafayette, IN. DA A1977-38(2),450-B, 462.

----, and J.E. Foster. 1983. Effect of leaf pubescence in wheat on the bird cherry oat aphid (Homoptera: Aphididae). J. Econ. Entomol. 76:1320–1322.

----, R.L. Gallun, F.L. Patterson, R.E. Finney, H.W. Ohm, and G.E. Shaner. 1981. Registration of Downy wheat. Crop Sci. 21:350.

Rochow, W.F. 1975. Barley yellow dwarf: Dependent virus transmission by *Rhopalosiphum maidis* from mixed infections. Phytopathology 65:99–105.

Rockwood, L.P., S.K. Zimmerman, and T.R. Chamberlin. 1947. The wheat stem maggots of the genus *Meromyza* in the Pacific Northwest. USDA Tech. Bull. 928. U.S. Government Printing Office, Washington, DC.

Rogers, C.E., R.D. Eikenbary, and K.J. Starks. 1972a. A review of greenbug outbreaks and climatological deviations in Oklahoma. Environ. Entomol. 1:664–668.

----, H.B. Jackson, and R.D. Eikenbary. 1972b. Responses of an imported coccinelled *Propylea 14-punctata* to aphids associated with small grains in Oklahoma. Environ. Entomol. 1:198–202.

Salt, G., G.F. Manson, and C.W. Farstad. 1945. The effect of the wheat stem sawfly (*Cephus cinctus* Nort.) on the heads of grain of infested stems. Ontario Entomol. Soc. Ann. Rep. 75:10–15.

Schillinger, J.A., Jr., and R.L. Gallun. 1968. Leaf pubescence of wheat as a deterrent to the cereal leaf beetle, *Oulema melanopus*. Ann. Entomol. Soc. Am. 61:900–903.

Sebesta, E.E., and E.A. Wood, Jr. 1978. Transfer of greenbug resistance from rye to wheat with X-rays. Agron. Abstr. American Society of Agronomy, Madison, WI. p. 61–62.

Slykhuis, J.T. 1953. Wheat streak mosaic in Alberta and factors related to its spread. Can. J. Agric. Sci. 33:195–197.

Smith, D.H., Jr., and J.A. Webster. 1973. Resistance to cereal leaf beetle in Hope substitution lines. p. 761–764. *In* E.R. Sears and L.M.S. Sears (ed.) Proc. 4th Int. Wheat Genet. Symp., Columbia, MO. 6–11 August. University of Missouri, Columbia.

Somsen, H.W., and W.H. Sill, Jr. 1970. The wheat curl mite, *Aceria tulipae* Keifer, in relation to epidemiology and control of wheat streak mosaic. Kans. Agric. Exp. Stn. Res. Pub. 162.

Sosa, O., Jr. 1981. Biotypes J and L of the Hessian fly discovered in an Indiana wheat field. J. Econ. Entomol. 74:180–182.

Starks, K.J., and R.L. Burton. 1977. Greenbugs: A comparison of mobility on resistant and susceptible varieties of four small grains. Environ. Entomol. 6:331–332.

----, ----, and O.G. Merkle. 1983. Greenbugs (Homoptera: Aphididae) Plant resistance in small grains and sorghum to biotype E. J. Econ. Entomol. 76:877–880.

----, ----, G.L. Teetes, and E.A. Wood, Jr. 1976. Release of parasitoids to control greenbugs on sorghum. USDA, ARS-S-91. U.S. Government Printing Office, Washington, DC.

----, and O.G. Merkle. 1977. Low level resistance in wheat to greenbug. J. Econ. Entomol. 70:305–306.

----, and K.A. Mirkes. 1979. Yellow sugarcane aphid: Plant resistance in cereal crops. J. Econ. Entomol. 72:485–488.

Stebbins, N.B., F.L. Patterson, and R.L. Gallun. 1982. Interrelationships among wheat genes H3, H6, H9, and H10 for Hessian fly resistance. Crop Sci. 22:1029–1032.

----, ----, and ----. 1983. Inheritance of resistance of PI 94587 wheat to biotypes B and D of Hessian fly. Crop Sci. 23:251–253.

Streams, F.A., and L.W. Cole. 1965. Wheat stem sawfly parasites, *Collyria calcitrator* and *Pediobius nigritarsis*, in eastern United States. J. Econ. Entomol. 58:303–306.

Streu, H.T., and J.B. Gingrich. 1972. Seasonal activity of the winter grain mite in turfgrass in New Jersey. J. Econ. Entomol. 65:427–430.

Teetes, G.L., C.A. Schaefer, J.R. Gipson, R.C. McIntyre, and E.E. Latham. 1975. Greenbug resistance to organophosphorous insecticides on the Texas High Plains. J. Econ. Entomol. 68:214–216.

Tyler, J.M., J.A. Webster, and E.L. Smith. 1985. Biotype E greenbug resistance in wheat streak mosaic virus-resistant wheat germplasm lines. Crop Sci. 25:686–688.

Viator, H.P., A. Pantoja, and C.M. Smith. 1983. Damage to wheat seed quality and yield by the rice stink bug and southern green stink bug (Hemiptera: Pentatomidae). J. Econ. Entomol. 76:1410–1413.

Vickerman, G.P., and S.D. Wratten. 1979. The biology and pest status of cereal aphids (Hemiptera: Aphididae) in Europe: A review. Bull. Entomol. Res. 69:1–32.

Von Wechmar, M.B. 1984. Russian aphid spreads gramineae viruses. p. 38–41. *In* M.C. Walters (ed.) Progress in Russian wheat aphid (*Diuraphis noxia* Mordw.) research in the Republic of South Africa. Tech. Comm. Dep. Agric. Repub. S. Afr. no. 191.

Wadley, F.M. 1931. Ecology of *Toxoptera graminum*, especially as to factors affecting importance in the Northern United States. Ann. Entomol. Soc. Am. 24:325–395.

Wallace, L.E., and F.H. McNeal. 1966. Stem sawflies of economic importance in grain crops in the United States. USDA Tech. Bull. 1350. U.S. Government Printing Office, Washington, DC.

----, ----, and M.A. Berg. 1973. Minimum stem solidness required in wheat for resistance to wheat stem sawfly. J. Econ. Entomol. 66:1121–1123.

Walters, M.C., F. Penn, F. du Toit, T.C. Botha, K. Aalbersberg, P.H. Hewitt, and S.W. Broodryk. 1984. The Russian wheat aphid. p. 72–77. *In* M.C. Walters (ed.) Progress in Russian wheat aphid (*Diuraphis noxia* Mordw.) research in the Republic of South Africa. Tech. Comm. Dep. Agric. Repub. S. Afr. no. 191.

Ward, C.R., E.W. Huddleston, J.C. Owens, T.M. Hills, L.G. Richardson, and D. Ashdown. 1972. Control of the Banks grass mite attacking grain sorghum and corn in West Texas. J. Econ. Entomol. 65:523–529.

Webster, J.A. 1977. The cereal leaf beetle in North America: Breeding for resistance in small grains. Ann. New York Acad. Sci. 287:230–237.

----, S.H. Gage, and D.H. Smith, Jr. 1973. Suppression of the cereal leaf beetle with resistant wheat. Environ. Entomol. 4:175–186.

----, and C. Inayatullah. 1984. Greenbug (Homoptera: Aphididae) resistance in Triticale. Environ. Entomol. 13:444–447.

----, and D.H. Smith, Jr. 1983. Developing small grains resistant to the cereal leaf beetle. USDA Tech. Bull. 1673. U.S. Government Printing Office, Washington, DC.

----, and ----. 1984. Effect of resistant wheat (*Triticum aestivum* L. em. Thell.) on cereal leaf beetle (*Oulema melanopus* (L.)) populations and damage to adjacent oats (*Avena sativa* L.). Protect. Ecol. 6:251–255.

----, ----, and R.P. Hoxie. 1982. Effect of cereal leaf beetle on the yields of resistant and susceptible winter wheat. Crop Sci. 22:836–840.

----, ----, E. Rathke, and C. E. Cress. 1975. Resistance to cereal leaf beetle in wheat: Density and length of leaf-surface pubescence in four wheat lines. Crop Sci. 15:199–202.

Wellso, S.G. 1973. Cereal leaf beetle: Larval feeding, orientation, development and survival on four small-grain cultivars in the laboratory. Ann. Entomol. Soc. Am. 66:1201–1208.

----, and R.D. Freed. 1982. Positive association of the wheat midge (Diptera: Cecidomyiidae) with glume blotch. J. Econ. Entomol. 75:885–887.

Wiese, M.V. 1977. Compendium of wheat diseases. American Phytopathological Society, St. Paul.

Wilde, G. 1981. Wheat arthropod-pest management. p. 317–327. *In* D. Pimentel (ed.) Handbook of pest management in agriculture, Vol. 3. CRC Press, Boca Raton, FL.

Wildermuth, V.L., and E.V. Walter. 1932. Biology and control of the corn leaf aphid, with special reference to the southwestern states. USDA Tech. Bull. 306. U.S. Government Printing Office, Washington, DC.

Wood, E.A., Jr. 1961. Biological studies of a new greenbug biotype. J. Econ. Entomol. 54:1171–1173.

----. 1965. Effect of foliage infestation of the English grain aphid on yield of Triumph wheat. J. Econ. Entomol. 58:778–779.

----. 1971. Designation and reaction of three biotypes of the greenbug cultured on resistant and susceptible species of sorghum. J. Econ. Entomol. 64:183–185.

----, E.E. Sebesta, and K.J. Starks. 1974. Resistance of 'Gaucho' triticale to *Schizaphis graminum* (Rond.). Environ. Entomol. 3:720–721.

----, and K.J. Starks. 1972. Effect of temperature and host plant interaction on the biology of three biotypes of the greenbug. Environ. Entomol. 1:230–234.

10 Quality of Hard, Soft, and Durum Wheats

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Wheat (*Triticum* spp.), civilization's basic food, is a complex, living, dynamic species that still hold many mysteries. These complexities, increased through the years by human selection, are the basis for the many uses of wheat. The most important food use is in the manufacture of flour for making bread, biscuit, and pastry products. Small amounts of wheat are converted into breakfast cereals, foods such as bulgur wheat, and semolina for the macaroni industry. Wheat also is a source of commercial starch and gluten. Wheat starch is used in the food and paper industries, in oil well drilling, as laundry starches, and in other products. It is no wonder that wheat quality means different things to different people.

Raw materials significantly different from the ordinary often do not have satisfactory quality characteristics, and usually require uneconomical modifications in the operations of wheat and flour processors. Storage and marketing of wheat are carried out by class, area, and market grades without regard to cultivar. Thus, the release of a cultivar with widely divergent properties may cause mixing and dilution of desirable traits.

Most quality characteristics important in processing are inherited and have been bred into the widely grown wheat cultivars accepted as stan-

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dards in industry and also in breeding and testing programs. Today's highly automated production techniques and procedures, in turn, are geared to the most prevalent wheat and flour attributes. Among breeding lines now being tested, however, the attributes often have a wide range.

The USDA maintains four regional quality laboratories cooperating with the several states. The functions, operations, and/or research of the laboratories have been reviewed by several workers (Barmore, 1959; Bode, 1959; Sollars and Barrett, 1964; Finney, 1964, 1971, 1978a, 1978b, 1984; Finney et al., 1982). Activities in the four laboratories provide background for much of the milling, chemical, physico-chemical, and baking work discussed in this chapter.

10–1 DEFINITION OF WHEAT QUALITY

Physical and chemical differences are strikingly great between different lots and cultivars of wheat. These differences have far-reaching effects and become the basis for what is loosely referred to as quality, whether the problem relates to breeding, testing and evaluating, cereal chemistry research, processing, or economics (Heyne and Smith, 1967; Reitz, 1967; Finney and Yamazaki, 1967; Pomeranz, 1971; MacMasters et al., 1971; Ziegler and Greer, 1971; Kasarda et al., 1971; D'Appolonia et al., 1971; Chung et al., 1978, 1982; Reed and Thorn, 1971; Fortmann and Joiner, 1971; Bloksma, 1971; Yamazaki and Lord, 1971; Irvine, 1971; Miller, 1974; Hanson et al., 1982; Finney, 1971, 1978b, 1979, 1984; Schruben and Seeborg, 1967). Actual quality of a wheat is the summation of effects of soil, climate, and seed stock on the wheat plant and the kernel components.

Johann Wolfgang von Goethe (1749–1832), a famous German poet, naturalist, anatomist, and physicist, stated: "Wood burns because it has the proper stuff in it; and a man becomes famous because he has the proper stuff in him." In the case of wood, *stuff* refers to chemical properties and components; in the case of a person, *stuff* refers to biochemical, biological, and cultural properties or qualities. What determines whether a wheat has the proper stuff in it?

Before the quality of several hundred pounds (or 3 to 4 lb, or only a few ounces) of wheat can be evaluated, quality must be defined and then measured by suitable methods. The basic definition of wheat quality usually varies from one class of wheat to another. The simplest definition of wheat quality probably is in terms of suitability: wheat that is desired has good quality and wheat that is not desired has poor quality. For example, the quality of a soft red or white wheat cultivar is defined in terms of its suitability for soft wheat milling and for the production of cakes, cookies, and crackers. The quality of a durum wheat is defined in terms of its suitability for semolina and macaroni production. Hard red winter and spring wheat quality is defined in terms of specific properties that determine suitability for hard wheat milling and bread production.

Thus, quality of any kind of wheat cannot be expressed in terms of a single property, but depends on several milling, chemical, baking, processing, and physical dough characteristics, each important in the production of bread, pastry, or pasta products.

10–2 QUALITY OF HARD (BREAD) WHEATS

10–2.1 Milling Properties

Important hard wheat milling properties are relative hardness or softness, weight per bushel of wheat, siftability of flour, break flour yield, middlings flour yield, total flour yield, flour ash content, and wheat-to-flour protein conversion. Most of those properties are determined during the experimental milling test, which can be performed on mills with capacities of a few hundred kg to as little as 25 to 50 g.

10–2.1.1 Hardness, Flour Yield, Protein Conversion, and Siftability

Although hardness can be determined by independent physical tests (Yamazaki and Donelson, 1983), it can be evaluated more accurately when determined as a part of the experimental milling test. Unusually hard or soft milling characteristics will usually be reflected in lower flour yields, which in turn are evaluated in relation to the wheat-to-flour protein conversions and ash contents. A wheat that is too hard usually requires more power and more than the normal number of break and reduction operations. The flour from such wheat usually will have a relatively high ash content. If a wheat is too soft, sifting properties probably will be unsatisfactory relative to the harder wheats. For example, certain stocks will tend to ball-up and not pass through the sieves or will require more sifting time. In addition, the mill flow will be altered as a result of an unusually high quantity of break flour. The ratio of middlings flour to break flour for micromilled bread wheats, an important criterion of hardness, generally is 1.1 to 1.5.

10–2.1.2 Flour Ash and Weight per Bushel

Neither flour ash nor flour yield can be properly assessed or evaluated without a knowledge of kernel plumpness, usually indicated by weight per bushel. Flour yield increases and flour ash decreases with increasing weight per bushel (Fig. 10–1). A flour yield of 70% and flour ash of 0.40% would be normal for 60-lb wheat, whereas a flour yield of 62.5% and flour ash of 0.60% would be expected for 50-lb wheat.

The samples of 'Pawnee' and 'Kaw' wheats in Fig. 10–1 possessed varying degrees of shriveling and did not represent any relatively plump wheats that were low in test weight because of weathering. Wetting and drying wheat reduces weight per bushel by decreasing kernel density and increases flour yield.

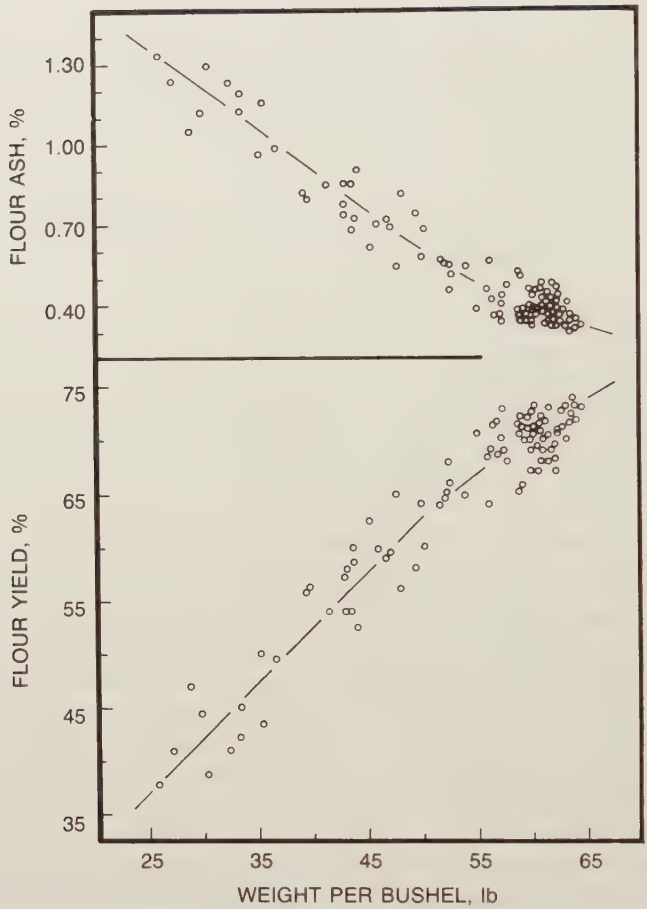

Fig. 10–1. Weight per bu vs. flour yield and flour ash for 'Pawnee' and 'Kaw' wheat harvested at varying stages of maturity at Manhattan, KS, in 1948, 1949, 1950, 1951, 1961, and 1962.

10–2.2 Prerequisites for Good Milling Quality

Specifically, a hard wheat of good milling quality should have normal bolting or sifting properties and therefore should be neither unusually hard nor soft. If, in addition, the wheat gives a normal yield of flour with a normal quantity of ash, almost invariably it will be suitable as a good milling hard wheat.

10–2.3 Breadmaking Properties

Wheat is too often regarded as merely a starch food crop, but it contains other valuable nutrients, notably proteins, lipids, minerals, and vitamins. The prominence of wheat is attributed not only to its nutritive value but also to its unique proteins. Unlike any other plant-derived food,

wheat contains water-insoluble gluten proteins, which enable a leavened bread dough to rise by forming a structure of minute cells that retain CO_2 produced during fermentation.

10-2.3.1 Protein Content of Flour

The flour proteins include gluten and nongluten proteins. The nongluten proteins are salt-soluble globulins and water-soluble albumins and glyco-proteins. The nongluten proteins are essential, because they greatly enhance the functionality of the gluten proteins.

To demonstrate and define breadmaking quality, it is necessary to relate the quality and quantity of the flour proteins to the other important functional (breadmaking) properties. The other properties are dough-mixing requirement and tolerance (physical dough properties), dough handling properties, water and oxidation requirements of flour, loaf volume potential, and crumb grain and crumb color of bread. Each of the other properties is a function of both the quality and quantity of flour protein.

10-2.3.2 Dough Mixing Requirement and Tolerance

The effect of quality and quantity of flour proteins on mixing (physical dough) properties can best be objectively determined by mixograms obtained on a mixograph (Finney and Shogren, 1972). The mixograph (Fig. 10–2) is composed of two pairs of planetary pins that revolve about three pins in a bowl that contains 10 g of flour and optimum water. As mixing proceeds, water is absorbed and the dough is progressively developed so that the resistance to the planetary pins passing through the dough increases and is recorded on paper moving about 19 mm (0.75 in) min^{-1}. Typical mixograms are illustrated in Fig. 10–3. Other things being equal, the peak or point of minimum mobility is the mixing requirement for optimum bread production.

A medium to medium-long mixing requirement, corresponding to the time to the peak of the top right mixogram in Fig. 10–3, generally is most desirable. Thereafter (left to right and top to bottom), mixing properties vary from questionable to unsatisfactory. Slope and width after the peak and stability of mixogram height on each side of the peak are indices of mixing tolerance. All flours used in Fig. 10–3 contained about 12% protein, so that the variations in mixing properties were functions of inherited protein quality.

At 7.5% protein (Fig. 10–4), the mixing time of 'Pawnee' was about 4 1/2 min; at 9.9% protein, mixing time decreased to 2 7/8 min; at 11.6% protein and above, mixing time was 2 1/8 to 2 3/8 min. Previous studies in our laboratory have shown that when protein decreases below about 12%, mixing time increases, primarily because the lower the protein below 12%, the greater the difficulty in forming a continuous phase of protein. The higher the protein, the higher the mixogram on the paper. Pawnee has a relatively short mixing time and mellow physical dough properties. 'Quivira/Tenmarq//Marquillo/Oro' (Fig. 10–5) has medium-strong to

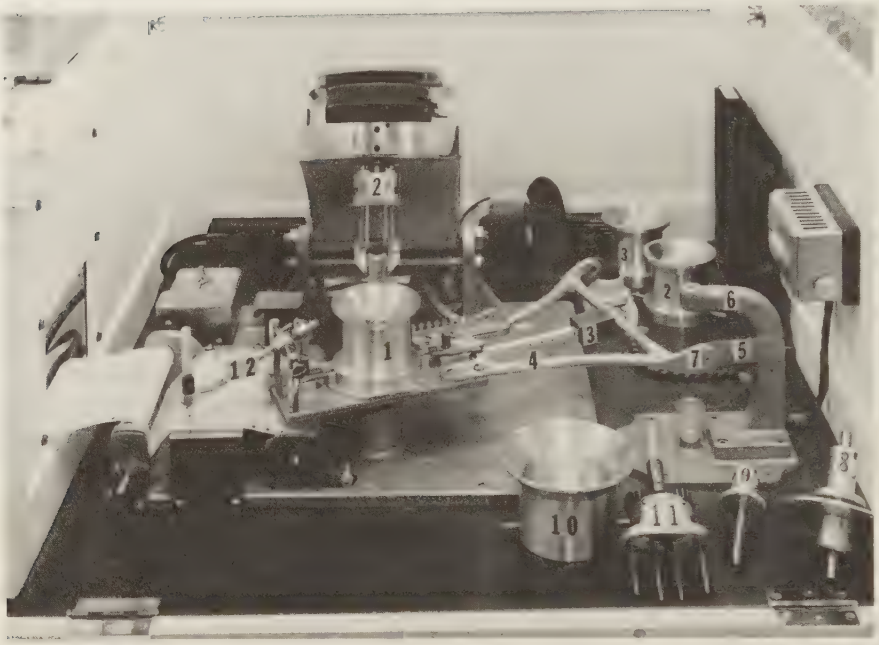

Fig. 10–2. Mixograph for recording mixing (physical dough) properties of 10-g samples of wheat flours. Bowl (*1*) is in operating position, directly below the raised mixing head (*2*) and its two planetaries, each with two pins that revolve in a predetermined pattern about three stationary pins in the bowl. The pen arm (*12*) with screw-in pen and black drawing ink exerts about 6 g of pressure on the recording paper. Three 10-g bowls are required for the efficient operation of the mixograph (bowls *2* and *3* are at the back-right corner). Parts *3* to *7* and *8* to *11* of the earlier 35-g model are described by Finney and Shogren (1972).

strong physical dough properties. At 8% protein, mixing time was about 10 min; at 10.4% protein, mixing time decreased to about 7 min; at 11.5% protein, mixing time decreased to 5 3/8 min; and at 13.1% and 16.2% protein, mixing times were about 4 5/8 min. As with Pawnee, mixing time greatly increased as protein content decreased below about 12%. Thus, both the quality and quantity of proteins affect the mixing (physical dough) properties of bread wheat flours.

10–2.3.3 Dough Handling Properties

Physical dough properties as shown in the mixogram generally are good indices of dough handling properties. Specifically, the desirability of handling properties usually decreases with decreasing mixing requirement and tolerance (Fig. 10–3), especially when mixing requirement is less than about 2 min. For times less than about 2 min, dough stability decreases and dough extensibility increases with decreasing mixing requirement. The flour represented by the top left mixogram of Fig. 9–3 has a questionably long mixing time and, unless blended with a physically weaker flour, gives a dough that usually is too strong physically and often is undesirably bucky (lacking extensibility).

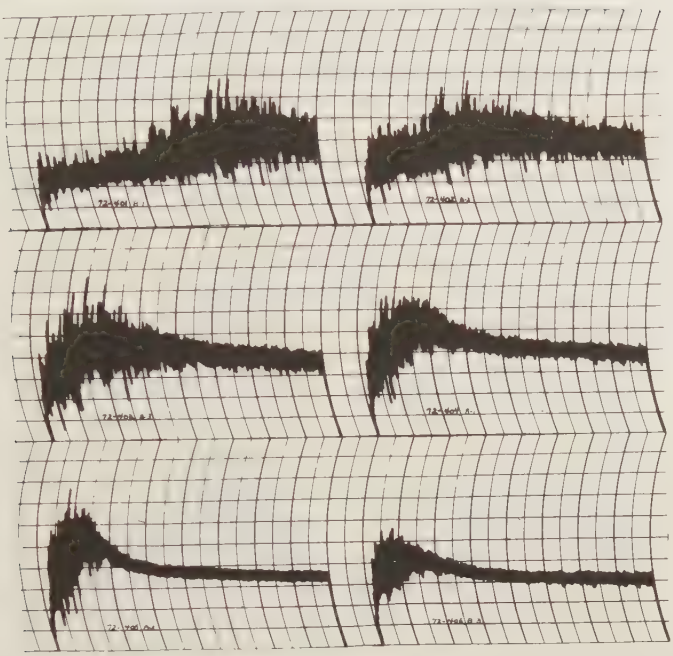

Fig. 10–3. Typical mixograms of hard winter wheat flours (10 g) that contained about 12% protein and vary in mixing requirement (time to peak or point of minimum mobility) and mixing tolerance (slope and width after peak, and stability of mixogram height on either side of peak). Major arcs are at 1-min intervals.

10–2.3.4 Water Requirement of Flour

As protein content increases within a cultivar, water absorption increases (Fig. 10–6). The regression lines in Fig. 10–6 form a fan-shaped family of lines that show the quality differences in water absorption at any given protein content (Finney, 1945). Thus, water absorption is a function of the quantity and quality of wheat flour proteins.

The data in Fig. 10–6, together with similar, unpublished, more recent data on many other cultivars of wheat, are the basis for a similar, updated family of regression lines. The following equations are for those who wish to reproduce the updated figure on cross-section paper:

$$Y = mX + b \qquad [1]$$

Given the values m = 1.5 and b = 43, with increases or decreases in m represented by Δm in the formulas, Eq. [1] becomes:

$$Y = 1.5X + 43;\ Y = (1.5 + \Delta m)X + 43 - 4.6666\ \Delta m$$
$$Y = (1.5 - \Delta m)X + 43 + 4.6666\ \Delta m$$

where

Y = flour bake absorption (14% moisture basis) with 4% nonfat dry milk (NFDM) in the formula, and

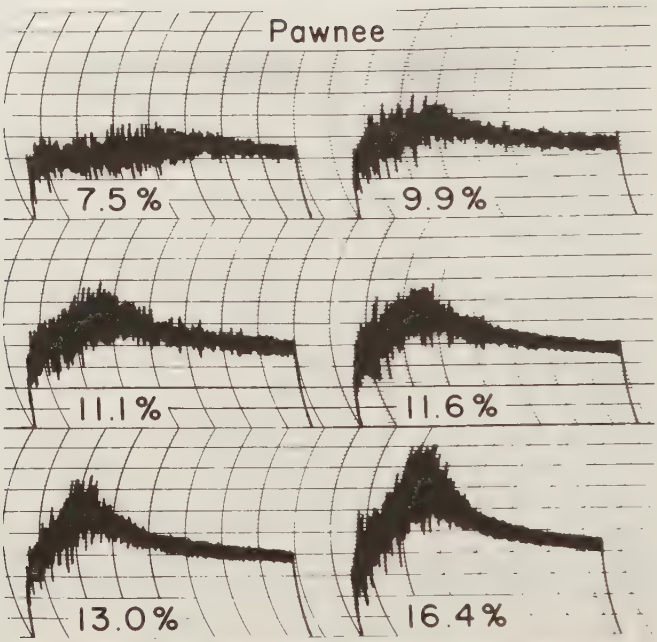

Fig. 10–4. Effect of flour protein content on mixogram mixing properties of 'Pawnee', a short-mixing hard winter wheat flour.

X = flour protein content (14% moisture basis).

When NFDM is omitted in the breadmaking formula, absorptions should be decreased three percentage points. The water absorption of NFDM is 75%.

10–2.3.5 Oxidation Requirement of Flour

Potassium bromate requirement (Fig. 10–7) of Pawnee varied from 1.5 mg $KBrO_3$ per 100 g of flour containing 8% protein to 6 mg at 16% protein (average about 4 mg). Kaw, a bread flour with medium-strong physical dough properties, required no bromate at about 8.5% protein and 3 mg at 16% (average about 1.5 mg). Pawnee, with mellow physical dough properties, required nearly three times as much oxidation as did Kaw. Thus, oxidation requirement of bread wheat flour is a function of both the quantity and quality of proteins.

Similar results were obtained for ascorbic acid, except that excessive amounts could be used to more than cover the range of oxidation requirements, because ascorbic acid is its own buffer against over-oxidation (Shogren and Finney, 1974).

10–2.3.6 Loaf Volume Potential

The fan-shaped family of regression lines for loaf volume and protein content of bread wheat flours was demonstrated by Finney (1943), Finney

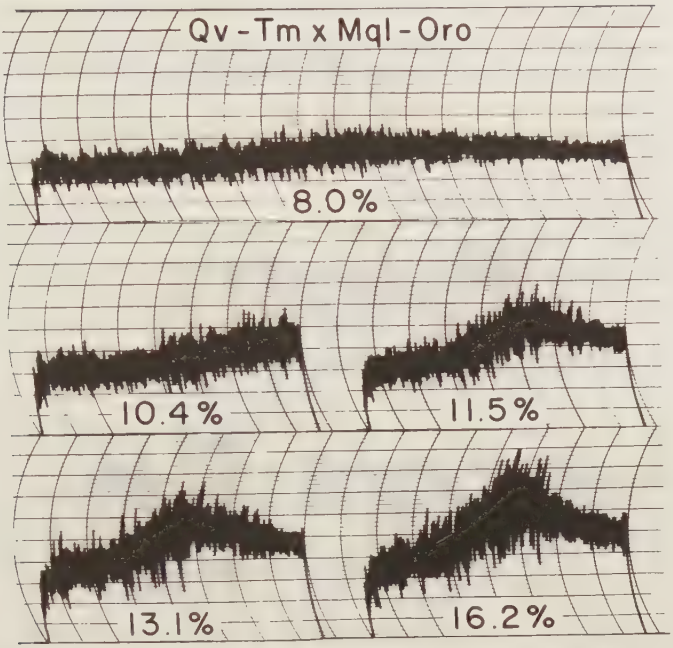

Fig. 10–5. Effect of flour protein content on mixogram mixing properties of 'Quivira/Tenmarq//Marquillo/Oro', a medium-long-mixing hard winter wheat flour.

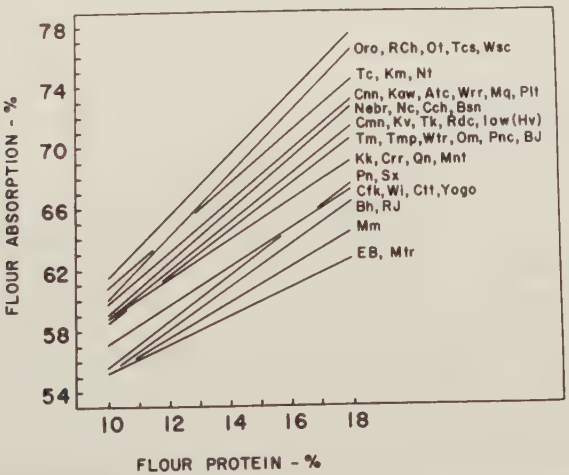

Fig. 10–6. Flour absorption vs. protein content regression lines for 42 hard winter and 3 hard spring wheat cultivars. Each cultivar regression line represents 25 to 100 samples harvested throughout the Great Plains during several crop years. Occasionally, experimental progenies fall on the top line or below the bottom line.

and Barmore (1948), and Finney and Fryer (1958). Those data, together with similar, mostly unpublished, more recent data on many other cultivars of wheat, are the basis for the different regression lines in Fig. 10–

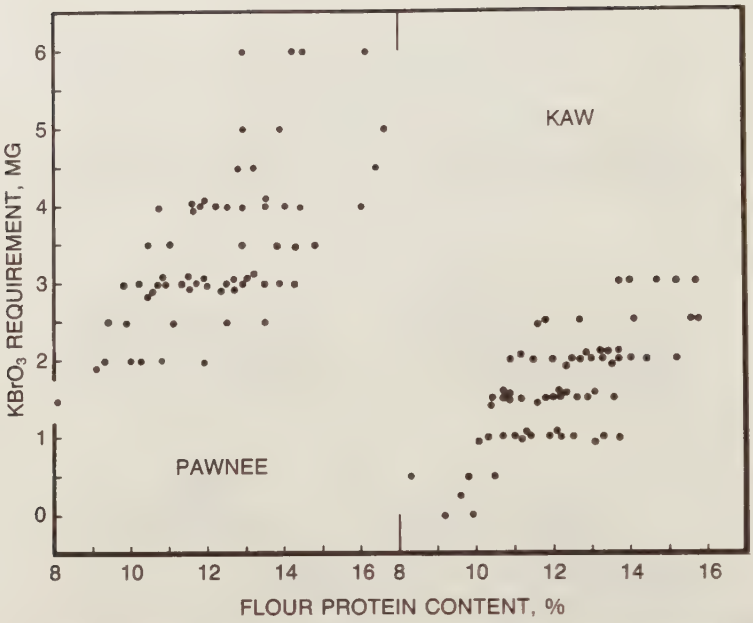

Fig. 10–7. Relation between oxidation ($KBrO_3$) required and flour protein content of 'Pawnee' and 'Kaw', short- and medium-long-mixing hard winter wheat flours.

8. There loaf volume increases with increasing protein content within a cultivar, and the regression lines for different wheat cultivars form a fan-shaped family of lines that are curvilinear below 12% flour protein. They meet at 300 cc and 0% protein (not shown in Fig. 10–8). The vertical distance between any two regression lines represents the difference in the gas retention of the gluten protein. Thus, loaf volume is a function of both the quantity and quality of flour proteins.

Loaf volumes of unknown wheat cultivars are evaluated against those of known cultivars after correcting or adjusting them to a suitable protein level with the aid of the data in Fig. 10–8. The loaf volume and protein content of a single sample of wheat flour establishes its relative gas-retention or protein quality.

The curvilinear regression equations for 0 to 12% flour protein content and the corresponding linear regression equations for 12% protein and above are given by Finney (1985).

10–2.3.7 Crumb Grain and Crumb Color of Bread

Good loaf volume potentials almost invariably are accompanied by at least satisfactory bread crumb grains that usually have relatively thick but satisfactory cell walls at the low protein levels, are best at the medium levels, and often are open but satisfactory at the high protein levels. Poor loaf volume potentials, instead, usually are accompanied by questionable to unsatisfactory bread crumb grains that have thick and unsatisfactory

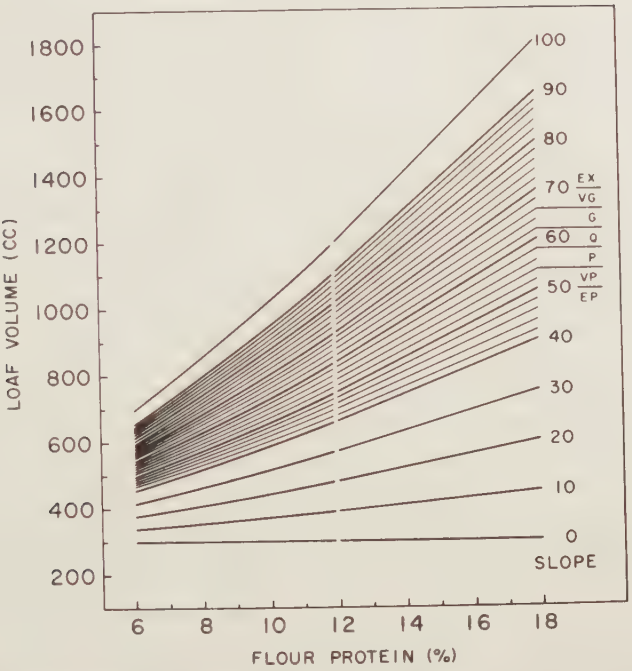

Fig. 10–8. Loaf volume (100 g of flour) vs. flour protein content curvilinear regression lines (to 12.0% protein) and their corresponding linear regression lines (above 12.0% protein) for correcting loaf volumes of wheat cultivars to a constant protein basis. Slope is the rate of change in loaf volume per 1% protein. Low protein samples should be corrected on the curvilinear lines. *EX* = excellent, *VG* = very good, *G* = good, *Q* = questionable, *P* = poor, *VP* = very poor, *EP* = exceptionally poor.

cell walls at the low protein levels, are best but questionable to unsatisfactory at the medium levels, and are often somewhat open but questionable to unsatisfactory at the high protein levels. Thus, both the quantity and quality of proteins affect the crumb grains of bread-wheat flours.

Good loaf volume potentials usually are accompanied by somewhat whiter or less creamy crumb colors than those that accompany poor loaf volume potentials, other factors being equal, because cell walls are less dense in loaves with good volume potentials. Also, within cultivars, crumb colors usually are not as white or are more creamy at the low protein levels than those at the higher protein levels, other factors being equal, because of the denser cell walls of low protein samples. Those crumb-color differences attributable to quality and quantity of protein are minor, however, compared to those associated with differences in type and quantity of pigments.

10–2.4 Prerequisites for Good Breadmaking Quality

A flour of good quality for breadmaking should have a high water absorption, a medium to medium-long mixing requirement, a small to

medium oxidation requirement, satisfactory mixing tolerance and dough handling properties, and good loaf-volume potential (considering protein content). Also, it should yield a loaf that has good internal crumb grain and color.

Subnormal breadmaking properties are associated with high temperatures above 32.2 °C and low relative humidities during the last 15 days before harvest (Finney and Fryer, 1958). Cultivars with longer mixing times, however, are more tolerant or resistant to the detrimental effects of the climatological factors than those with shorter mixing times. Thus, resistance to the damaging effects of high temperature and drought during the fruiting period is another important but special cultivaral characteristic that is taken into account by selecting cultivars that have medium to medium-long dough mixing requirements.

Good quality, physically strong-type wheats must be considered from both the breeding and the commercial standpoints. A genetically good quality, strong wheat is not a good quality, physically strong wheat by commercial standards unless it has a sufficient quantity of protein. Thus, genetically good quality, hard wheats could be grown throughout all of the Great Plains, but if protein content were low, the wheats essentially would be useless and otherwise commercially of poor quality. The protein content is a limiting factor. The principal difference between the hard winter and hard spring wheat crops is that the latter usually averages two to three percentage points higher in protein content. The commercial quality of hard winter wheat has been improved in recent years by breeding high protein cultivars that have raised the protein level by about 1% (Finney, 1978a).

10–2.5 Milling Methods

Upon receipt samples of wheat are appropriately fumigated, after which they are aerated, cleaned, mixed, and subsampled for chemical analysis and milling. Test weights are determined on the milling subsamples.

Most hard winter wheats are tempered to 15% moisture 18 to 24 h before milling. Harder than normal wheats of the 'RedChief' and 'KanKing' type are tempered to 16% moisture. Softer than normal wheats such as 'Triumph' are tempered to 14.5% moisture, and some crosses with soft wheats receive as little as 13% temper water.

10–2.5.1 Macromilling (1 kg or More)

After recording the weight, each 1.5-kg, tempered sample of wheat is subjected to the Allis experimental mill flow given in Fig. 10–9. To keep ash contents of straight-grade flours above 0.40%, the overs of the 26 and 54 (coarse and fine bran, respectively) from the fourth break are passed through the fourth break before going to feed. The mill has six stands of rolls that include three pairs of corrugated break rolls, two pair of smooth

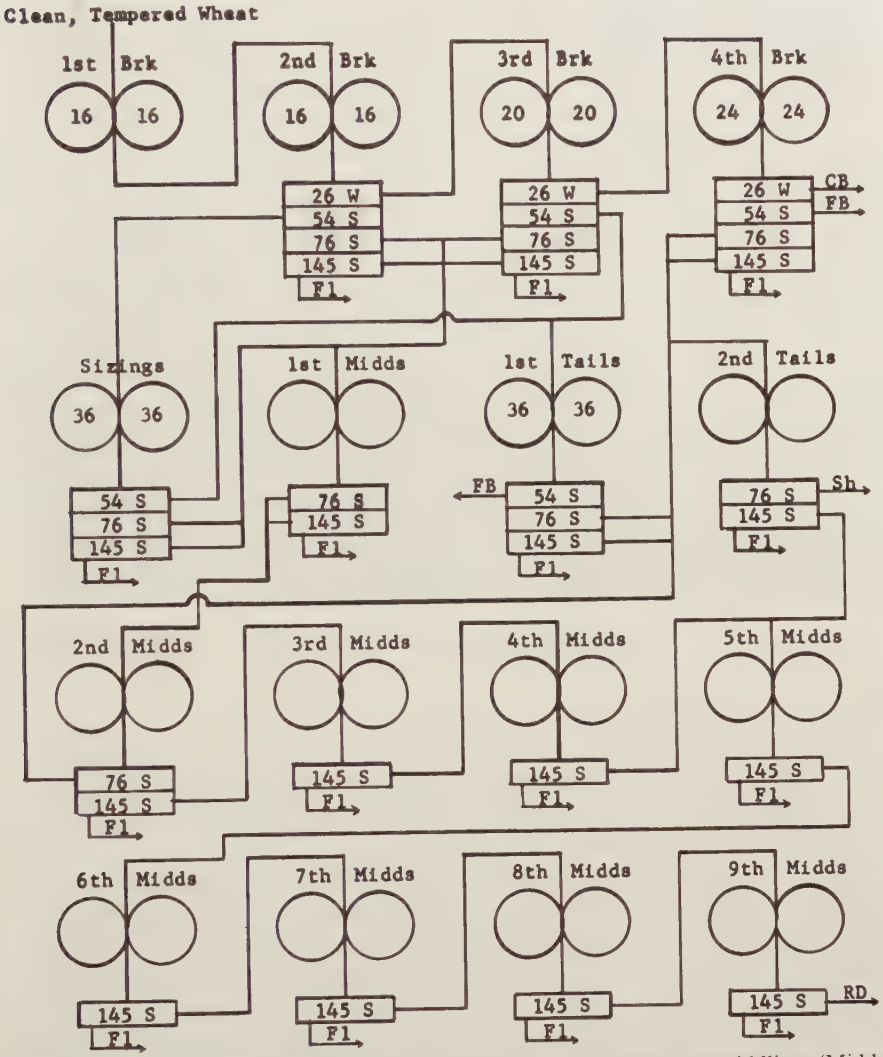

Fig. 10–9. Allis experimental mill flow of break (Brk) and reduction or middlings (Midds) stock, together with roll corrugations per inch and sieve openings per linear inch. All sieves are of stainless steel wire (*S*), except the 26 wire (*W*). Roll differential for all breaks is 2.5 to 1 and for sizings, tailings, and all middlings is 1.5 to 1. *CB*, *FB*, *Sh*, *RD*, and *Fl* are abbreviations for coarse bran, fine bran, shorts, red dog, and flour, respectively.

rolls, and one pair of sizings and tailings rolls. Two stands of rolls with a sifter between are mounted on each of three tables (Fig. 10–10). Weights of coarse plus fine bran, shorts, red dog, break flour, middlings flour, and total flour are recorded. Flour is rebolted over a 9XX flour cloth. After blending for 5 min, a 50-g flour subsample is taken for chemical analysis prior to baking.

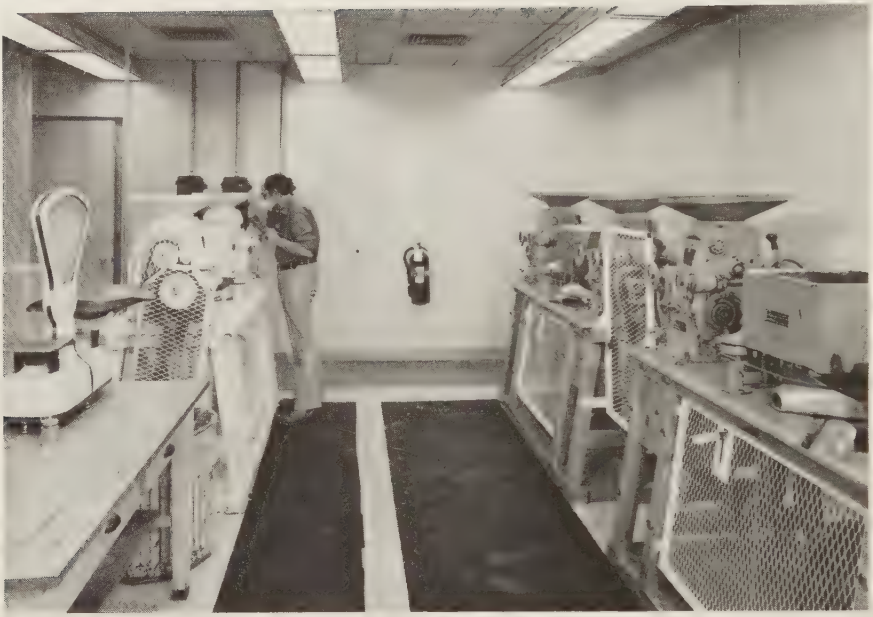

Fig. 10–10. View of Allis-Chalmers experimental mills. Two stands of rolls with a sifter between are mounted on each of three tables. One stand of rolls on the right is not visible.

10–2.5.2 Micromilling (40-100 g)

The ability to mill and record precisely the important milling properties of 40- to 100-g samples of early generation wheat progenies (Finney, 1964) greatly accelerates the release of new hard wheat cultivars that have superior agronomic, milling, and breadmaking properties.

Each 40- to 100-g tempered sample of wheat, after its weight is recorded, is subjected to the micromill flow shown in Fig. 10–11 (Finney and Yamazaki, 1946; Finney, 1964; Finney and Bolte, 1985). The micromill, which yields flours comparable to those obtained on larger and longer-extraction experimental mills, is composed of pre-break rolls of the Tag-Heppenstall moisture meter, a Brabender three-break milling head, two Ro-Tap sifters, and a Brabender three-reduction milling head (Fig. 10–12). After passing the pre-broken wheat through the break rolls, the overs of the 35 are removed after sifting 2.0 min, and the overs of the 65 and 100 are removed after sifting an additional 2 min. Stock through the reduction rolls for the first time is sifted 2 min. Softer-than-normal wheats may require 3 min. Stock through the reduction rolls the second time is sifted 2 min. Six samples can be in the process of milling at any given time, and about eight samples per h can be milled by a single operator. With a second person to weigh the fractions, about 12 samples per h can be milled. Flour yields of 71 ± 4% and flour ash contents of 0.40 ± 0.05% are typical, and depend on kernel plumpness, hardness, and cultivar. If necessary, flour is rebolted over a 9XX flour

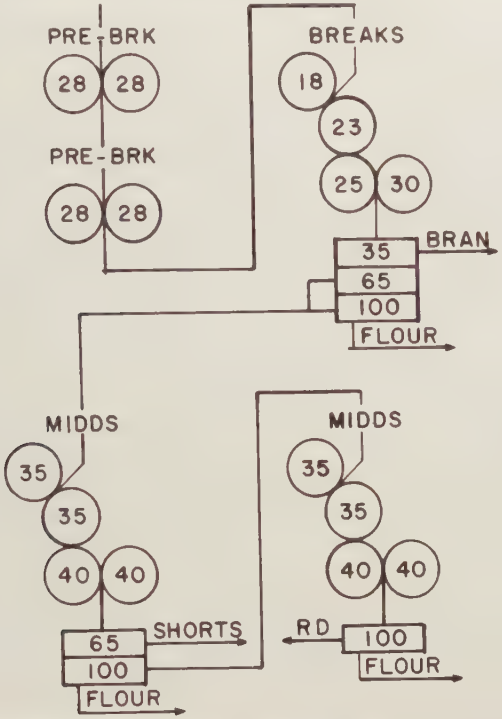

Fig. 10–11. Experimental micromill flow of pre-break, break, and reduction or middlings (Midds) stock, together with roll corrugations per inch and Tyler sieve openings per linear inch. Pre-break roll spiral is zero. Going from top to bottom, break roll spirals are 1.5, 1.0, 1.0, and 0.5 inch per foot, and reduction or middling roll spirals are 1.0, 0.5, 1.0, and 0.5 inch per foot. Distances between pre-, first-, second-, and third-break rolls are 0.063, 0.03, 0.0035, and 0.002 inch, respectively. Distances between first-, second-, and third-middling rolls are 0.0015, 0.002, and 0.0015 inch, respectively. The speed of the pre-break drive roll is 31 rpm. From top to bottom, speeds of break rolls are 1200, 545, 1200, and 545 rpm, and speeds of middling rolls are 1180, 535, 1180, and 535 rpm. Differential of pre-break rolls is 1.0. Differential of first-, second-, and third-break rolls and of first-, second-, and third-middling rolls is 2.2. *RD* is an abbreviation for red dog.

cloth before blending for 5 min. Moisture and protein analyses are made prior to running mixograms. Relative hardness or softness is observed and noted after breaking, reducing, and sifting operations (Finney and Bolte, 1985). Undesirably hard or soft milling characteristics usually are reflected in lower flour yields, which in turn are evaluated relative to flour ash. Flour ash, however, usually is determined only on samples found to have desirable mixogram mixing properties.

10–2.6 Breadmaking Methods (Recommended)

For the manifestation of loaf volume and crumb grain potentials and other functional properties, an analytical baking test such as the one developed by Finney and Barmore (1943, 1945a, 1945b, 1948) and Finney (1945, 1984) is required. In that test, mixing time, oxidation level, fer-

Fig. 10–12. View of experimental micromill primarily for 40 to 100 g of wheat. As little as 15 to 20 g or several hundred grams readily can be milled. Starting at the far right and going counter clockwise are the pre-break rolls of the Tag-Heppenstall moisture meter, a timer, a Brabender 3-break milling head, two Ro-Tap sifters, a timer, a Brabender 3-reduction milling head, a rebolt sifter, sample cans, a balance, and typical yields of bran, shorts, red dog, break flour, first reduction flour, and second reduction flour.

mentation time, and water absorption are optimized and balanced. Yeast is added at a level that is optimal and not limiting for the fermentation time. Shortening, sugar, and malt are added in excess so that none becomes limiting. Sufficient salt is used to produce an optimal effect, but not enough to impair gas production. Loaf volume and crumb grain potentials are measured accurately and at a maximum of differentiation between good and poor volume wheat flours. The optimized test can be performed with the analytical precision of most generally accepted biological assays.

Figures 10–13 and 10–14 illustrate the effects and importance of dough ingredients on loaf volume and crumb and on differentiation between good and poor quality samples. RBS-76 good quality flour (100 g, 14% moisture basis) and water (as needed) formed a dough, but the loaf volume was only 228 cc, equal to that of the dough volume after mixing. Leavening with 7.2% yeast increased loaf volume to 530 cc. Adding 0.5% barley malt (52 dextrinizing units per g, 20°C) and then both malt and 1.5% salt to flour, water, and yeast further increased loaf volume to 706 and 778 cc, respectively, but all crumb grains were unsatisfactory to varying degrees. When 3% shortening and 50 ppm ascorbic acid were added to the five basic ingredients, a loaf of excellent volume (1044 cc) and crumb grain was produced (Fig. 10–13).

Volumes of loaves 1, 2, and 3 of the poor quality 76-412 flour (Fig. 10–14) were significantly less than those of the corresponding loaves of

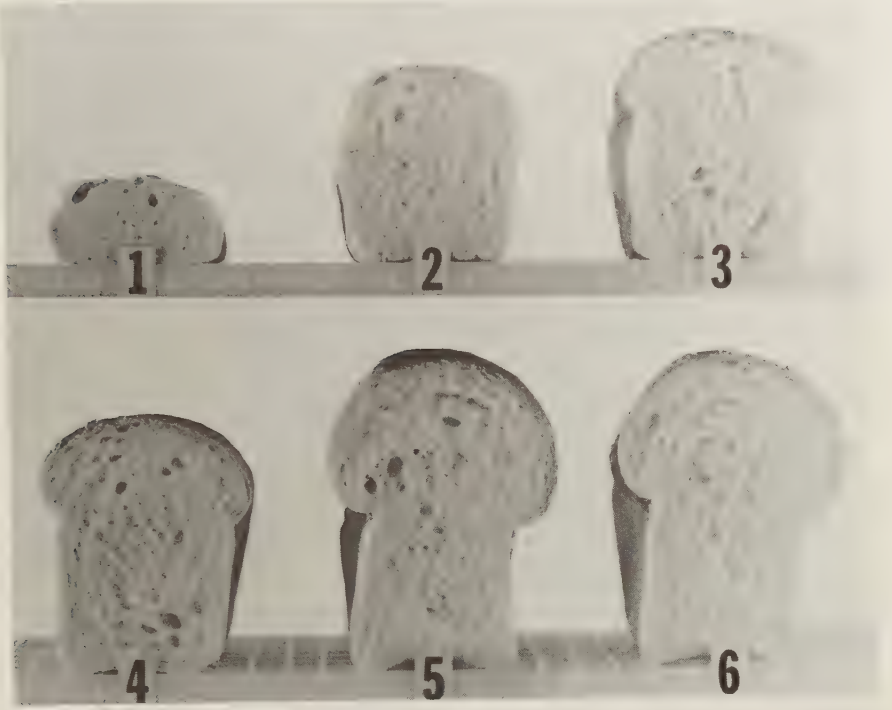

Fig. 10–13. Loaf volumes for cut loaves of bread made from 'RBS-76' good-quality flour and (*1*) water (228 cc) plus: (*2*) yeast (530 cc); (*3*) yeast and malt (706 cc); (*4*) yeast, malt, and salt (778 cc); (*5*) yeast, malt, salt shortening, and ascorbic acid (1044 cc); and (*6*) yeast, malt, salt, shortening, ascorbic acid, and 4% of soy flour (1033 cc), all with 70 min of fermentation. See Finney, 1984, Table III.

RBS-76. Loaf 4 of 76-412, containing flour, water, yeast, malt, and salt, was 134 cc less than loaf 4 of RBS-76 (644 vs. 778 cc); loaf 5 of 76-412, containing also shortening and ascorbic acid, was 320 cc less than loaf 5 of RBS-76 (724 vs. 1044 cc). Thus, the poor responses of poor quality gluten proteins to breadmaking ingredients and the good responses of good quality gluten proteins define a criterion of quality.

10–2.6.1 One hundred grams of Flour: Formula and Techniques

For most purposes, the breadmaking method includes mixing to minimum mobility (optimum) at about 100 rpm or more, optimum water (depending on quantity and quality of protein), and 50 ppm of ascorbic acid (an excess in the absence of NFDM, but ascorbic acid is its own buffer against over-oxidation). Additional formula ingredients are 100 g of flour (14% moisture basis), 3.5 or 5.3 g of compressed yeast (for 120 or 90 min of fermentation, respectively), 6 g of sugar, 1.5 g of salt, 3 g of shortening or equivalent surfactant, and 0.25 g of barley malt (about 50 dextrinizing units per g, 20 °C). Fermentation times for first punch, second punch, and pan depend on total time (Table 10–1). For 120 min

Fig. 10–14. Loaf volumes for cut loaves of bread made from '76-412' poor-quality flour and (*1*) water (205 cc) plus: (*2*) yeast (460 cc); (*3*) yeast and malt (669 cc); (*4*) yeast, malt, and salt (644 cc); (*5*) yeast, malt, salt, shortening, and ascorbic acid (724 cc); and (*6*) yeast, malt, salt, shortening, ascorbic acid, and 4% of soy flour (721 cc), all with 70 min of fermentation. See Finney, 1984, Table III.

Table 10–1. Time intervals (during breadmaking) between dough mixing, first punching, second punching, and panning for various fermentation times and the corresponding yeast concentrations, together with approximate proof times.

Fermentation time	Yeast	Punching†		Panning†	Approximate proof time‡
		First	Second		
min	%	min			
180	2.0	105	50	25	60 ± 2
150	2.5	87	42	21	51 ± 2
120	3.5	69	34	17	42 ± 2
90	5.3	52	25	13	33 ± 2
70	7.2	40	20	10	27 ± 2
60	8.6	35	17	8	24 ± 2

†Times to first and second punchings and panning of straight doughs are about 58, 28, and 14% of each fermentation time, respectively.
‡Proof times will vary additionally with the type and potency of the yeast.

of fermentation, proof 42 ± 2 min at 30 °C; for 90 min, proof 33 ± 2 min. These are the times required to proof the controls, containing about 12.5% protein, to a height of 7.8 cm. The proof height varies with the flour protein content of the controls (Fig. 10–15). Bake for 24 min at 215°C. Loaves are weighed immediately upon removal from the oven. Immediately thereafter, volumes are determined by rapeseed displacement (Fig. 10–16). Additional related details are given by Finney, 1945, 1984; Finney and Barmore, 1943, 1945a, 1945b; Finney et al., 1976; and Bruinsma and Finney, 1981.

Flours that have short to medium-short mixing times may need 10 ppm of bromate in addition to 50 ppm of ascorbic acid. Flours that have medium-long to long mixing times and other strong physical dough properties are likely to need only 10 to 20 ppm of ascorbic acid. Loaf volumes are not likely to suffer from the full 50 ppm of ascorbic acid, but crumb grains probably would be somewhat overdeveloped.

Flours that require 10 ppm of bromate generally require the highest amounts when ascorbic acid is omitted. The recommended method can be used to predict bromate requirement when ascorbic acid is omitted, but it would be desirable to add 4% of NFDM as a buffer against overbromating. If NFDM is not added in the recommended method, then flours that have medium-long to long mixing requirements will require no bromate, or only a little; the bromate should be added in 0.25- to 0.5-mg increments per 100 g of flour (or, when mixing times are short, 1-mg increments). When NFDM and an average of 30 ppm of bromate were used in the first replicate of all wheat cultivars baked in the Hard Winter Wheat Quality Laboratory, bromate requirement for subsequent bakes

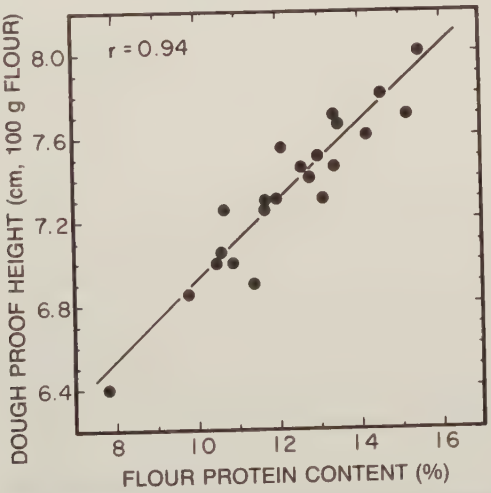

Fig. 10–15. Dough proof height and flour protein content of 22 location composites. Each contained equal quantities of 25 cultivars of hard winter wheat, each grown at the 22 locations in the Southern Great Plains in 1973. Add 4 mm to these values to adjust for changes in the properties and concentration of yeast since 1973.

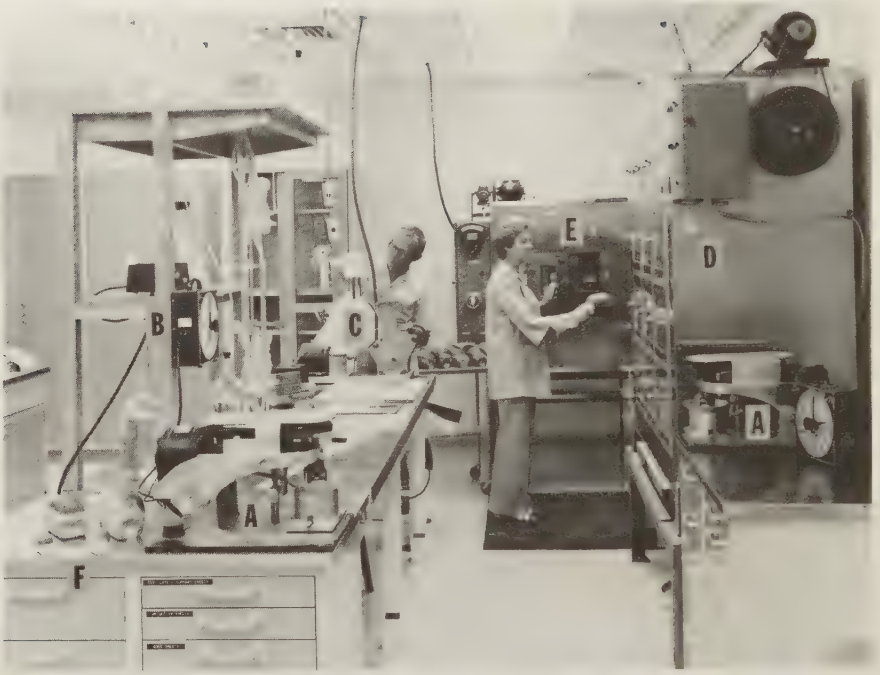

Fig. 10–16. View of the experimental bakery in the Hard Winter Wheat Quality Laboratory at the U.S. Grain Marketing Research Laboratory, Manhattan, KS. Dough mixers (100 g of flour) are at *A*. After wheat flour and shortening are added to mixing bowl, solutions of sugar-salt, diastatic malt, yeast, ascorbic acid, and sometimes $KBrO_3$ are added from the dispensing stand *B*. At *C* are sheeting (punching) rolls and a dough about to be molded and panned, prior to placing in the fermentation and proofing cabinet *D*. A loaf has been removed from the baking oven at *E*, after which loaf volume is determined by dwarf rapeseed displacement with a volumeter (not visible, on a table at the end of the fermentation cabinet). In the lower left hand corner above *F* are 100-g and 10-g (flour basis) loaves baked from good (*right*) and poor (*left*) quality flours. For breadmaking with 10 g of flour, appropriate dough mixers, portable dispensing stand, dough molder, bread pans, and volumeter for 10 g of flour quickly replace the 100-g equipment (Shogren and Finney, 1984).

was predicted from optimum mixing time. Flours that have short mixing requirements generally have high bromate requirements, and those with long mixing requirements have low requirements (Finney and Yamazaki, 1967).

In formulas that contain relatively high levels (8 to 12%) of soy flour in place of wheat flour, sugar should be omitted and the barley malt doubled or trebled, since high levels of soy flour produce excessive browning in the presence of sucrose. Also, both 3% of shortening and 0.5% of a surfactant such as sodium stearyl-2-lactylate should be added.

For additional details on basic concepts, the subjective determination of optimum mixing time, breadmaking equipment, dispensing of ingredients, and important considerations in experimental breadmaking, refer to Finney, 1984; Finney et al., 1976; and Magoffin et al., 1977.

10–2.6.2 Ten grams of Flour: Formula and Techniques

For the 10-g breadmaking method, formulation amounts for the 100-g method are reduced by a factor of 10. Other details given for 100 g of flour also are applicable, except that proof time of doughs that contain 10 g of flour is the time required to proof the controls, containing about 12.5% protein, to 4.1 cm proof height. Proof times for 90 and 120 min of fermentation are about 35 and 44 min, respectively, and will vary with the type and potency of the yeast.

Flour samples (10 g, 14% moisture basis) are weighed the day before into small plastic screw-cap jars. Additional ingredients in the form of powder or semisolids, other than those in the routine formulation, are blended immediately with each flour. On the day of baking, the flour is transferred to the mixing bowl, shortening is dispensed with the rod and tube, and liquid ingredients are added by means of the dispensing apparatus. Each dough is mixed to the point of minimum mobility, removed from the mixer, and placed in a bowl that is covered and then placed in the fermentation cabinet (30 °C). Fermentation is 90 or 120 min. Proof time is the time required to proof the controls to 4.1 cm. Doughs are punched after 52, 77, and 90 min or after 69, 103, and 120 min for the 90- and 120-min fermentations, respectively (Table 10–1). After the final punch, the ribbon of dough is placed on and toward one end of the runner and ahead of the molder. Then the end of the dough nearest the front of the molder is turned up to form an 'L' that makes contact with the curling plate. Molding is accomplished in about 2 s by pushing the molder along the runner (Fig. 10–17; Shogren and Finney, 1984). The molded dough is placed in a bread pan, returned to the fermentation cabinet, and proofed for the time required for the controls to proof to 4.1 $\pm$ 0.1 cm. After adequate proofing, doughs are baked for 13 min at 232°C. After removal from the oven, loaves are immediately weighed and then placed on a wire grid for about 2 h before volumes are determined by dwarf rapeseed displacement.

Duplicate determinations are made and averaged if within $\pm$ 0.5 cc; additional determinations are made if duplicates do not agree within 0.5 cc. Loaves are cut and scored after loaf volume determinations are made. Loaf volume differences of about 3 cc usually are significant at $P = 0.05$. For additional details on basic concepts, the subjective determination of optimum mixing time, breadmaking equipment, dispensing of ingredients, and important considerations in experimental breadmaking on 10 g of flour, refer to Shogren and Finney, 1984; Finney, 1984; Finney et al, 1976; and Magoffin et al., 1977.

10–2.7 Methods For Predicting Functional Properties

Many tests have been developed in the past to study wheat quality. These include simple chemical, physical, and physico-chemical tests, physical dough-testing equipment and techniques, and baking methods and techniques. A survey of all these tests has been published (Miller

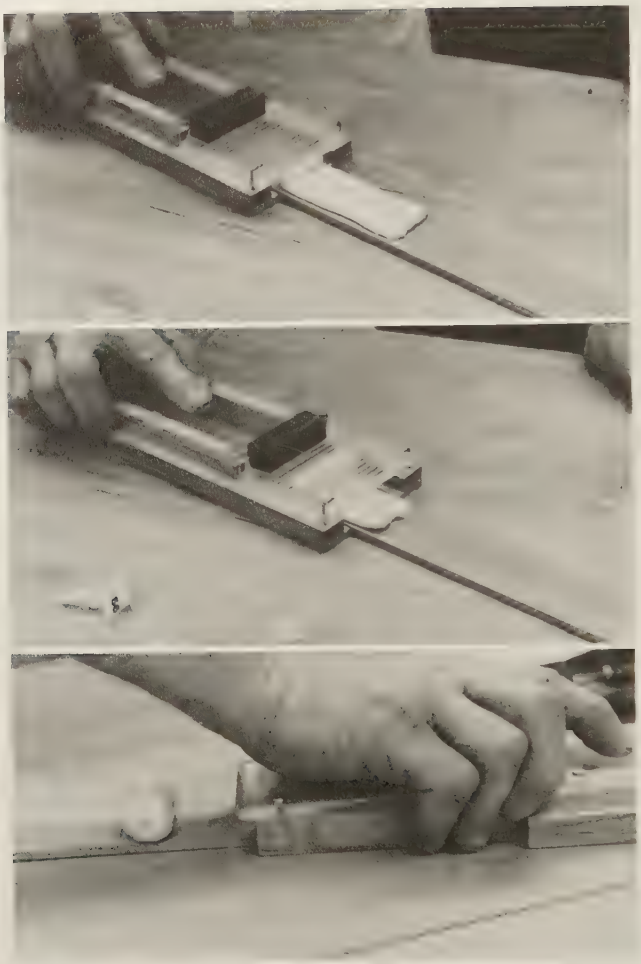

Fig. 10–17. Molding bread dough from 10 g of flour: initiating (*top*), curling step (*center*), and completion (*bottom*).

and Johnson, 1954). Certain of them still are useful to varying degrees today for the determination of specific flour properties.

10–2.7.1 Near-Infrared Reflectance Spectroscopy (NIRS)

10–2.7.1.1 Protein and Moisture Content. Williams (1975) reported on the application of near-infrared reflectance spectroscopy (NIRS) to the analysis of cereal grains and oilseeds. Williams et al. (1982) studied the influence of temperature on the estimation of protein and moisture contents in wheat by NIRS and developed a simple, practicable, inexpensive procedure for the correction of results to ambient room temperature. Many laboratories throughout the world are using NIRS to obtain quickly the approximate moisture and protein content of wheat

and flour samples. The NIRS has greatly speeded up, and reduced in cost, moisture and protein analysis for the many hundreds of early generation progenies of wheat that are micromilled and evaluated for breadmaking quality each year at the Hard Winter Wheat Quality Laboratory.

10-2.7.1.2 Relative Hardness. Bruinsma and Rubenthaler (1978) estimated lysine and texture in cereal grains by NIRS, and Williams (1979) screened wheat for hardness by NIRS. The NIRS has been used in the early 1980s in the Hard Winter Wheat Quality Laboratory to determine hardness of many hundreds of early generation progenies of wheat, so that they could be properly tempered for micromilling. Values for hardness, moisture, and protein content were obtained quickly on the same sample.

10-2.7.2 Particle Size Index

Yamazaki and Donelson (1983) found that higher moisture content was associated with greater softness as determined by the particle size index (PSI). They adjusted PSI values to a uniform moisture content by means of a fan-shaped family of regression lines. Particle size index values obtained by grinding the wheat samples through a properly calibrated burr-type grinder were highly significantly correlated with break-flour yield from Allis- Chalmers laboratory millings, whereas PSI data for a comminution grinder were not significantly correlated with milling data.

10-2.7.3 Doughball Test

The wheat-meal-time-fermentation (doughball) test is well known in the USA as a test for differentiating between long, medium, and short doughball times of early generation wheat progenies from long- and short-time parents. Doughball time, in general, is significantly correlated with loaf volume. The stronger-type (medium-long mix time) wheats often have medium-long to long doughball times. The test has been widely used in Germany, France, and Argentina to grade wheat (Miller and Johnson, 1954). Recently, linear correlations of loaf volume and dough mixing time to Pelshenke value indicated that Pelshenke value is largely a function of the environment and is related to quality and quantity of protein only to a limited and impractical extent (Monsivais et al., 1983).

10-2.7.4 Alveograph

The alveograph (Chopin extensimeter) has been used extensively in France for testing French flours, but has gained little or no popularity in the USA as a physical test for hard wheat flours. It uses air pressure to blow a bubble from a disc of dough. A recording manometer is employed as the bubble is expanded to the breaking point. The height of the curve is a measure of the dough's initial resistance to extension (forming the bubble). The length of the curve is an index of dough extensibility and

gas retention. The final curve is made by averaging five replicate curves from a 250-g sample. A modified alveograph has been devised for relatively small, 15-g samples of hard winter wheats (Shogren et al., 1963a). Alveogram length by the modified method is highly correlated with loaf volume and is particularly useful in predicting loaf volume of hard winter wheat flour when mixing or oxidation requirement is taken into account (Shogren et al., 1963b).

10-2.7.5 Sedimentation Test

The sedimentation test is used for estimating the quality of small samples of wheat. Coarsely ground wheat is sifted to remove most of the bran, and 3.2 g of the crude flour is suspended in water and treated with lactic acid in a graduated cylinder (AACC, 1983). Volume of the swollen sediment, after a 5-min standing period, is the sedimentation value. The small sample size required and the speed and simplicity of the test have appealed to many plant breeders.

10-2.7.6 Farinograph

The farinograph is one of the most widely used physical dough-testing instruments in the world. It measures plasticity and mobility of dough that is subjected to prolonged, relatively gentle mixing at constant temperature. Resistance offered by the dough to mixing blades is transmitted through a dynamometer to a pen that traces a curve on a kymograph chart (Brabender, 1965). Farinograms provide accessory information on such properties as absorption, optimum mixing time, and mixing tolerance. The farinogram may be used to estimate absorption and mixing time of a flour to be baked, provided the necessary correlations have been established (Shellenberger et al., 1970).

10-2.7.7 Mixograph (10 g)

The 10-g mixograph (Finney and Shogren, 1972), a miniature high-speed recording dough mixer, is used in many laboratories in the USA and elsewhere. It is a particularly useful instrument for the objective determination of some and the prediction of other important breadmaking properties of wheat cultivars.

10-2.7.7.1 Mixing Requirement (Time) and Tolerance. Two important breadmaking properties, mixing requirement (or time to the point of minimum mobility of dough) and mixing tolerance are objectively determined from the mixogram obtained on a 10-g mixograph. Correlation coefficients for bake mixing time vs. mixogram mixing time averaged $r = 0.95$ for 16 groups totaling 438 samples of typical hard winter wheats harvested throughout the Great Plains during three crop years (Finney and Barmore, 1945b). Also, mixograph mixing time is much more highly correlated with experimental bake mixing time than is far-

inograph mixing time (Miller et al., 1956; Shellenberger et al., 1970). Mixing tolerance is a function of the slope and width of the mixogram after the peak and the stability of mixogram height on either side of the peak. The greater the slope and the less the width, the poorer the mixing tolerance (considering flour protein content, Fig. 10–4 and 10–5). The longer the mixing time, in general, the better the mixing tolerance.

10–2.7.7.2 Oxidation Requirement vs. Mixing Requirement. Data in Fig. 10–18 show that oxidation requirement decreases materially with increasing mixing time or requirement and reaches a minimum at about 5 min, beyond which oxidation requirement is approximately constant. Thus, oxidation requirement can be predicted from a knowledge of mixing requirement and flour protein content.

To minimize the effect of protein content variations, Fig. 10–18 represents only groups of composite samples that had mean protein contents of 12 to 13%. Cultivar composites represent a wide range of quality characteristics and were made up of hard winter wheats harvested throughout the Great Plains in 1959 to 1962. Although the mean flour protein of the sample groups varied from only 12 to 13%, the variation in protein within each group was about ± 1% of the mean. Accordingly, at least part of the deviation about the imaginary regression is attributable to a total protein content variation of about 11 to 14%.

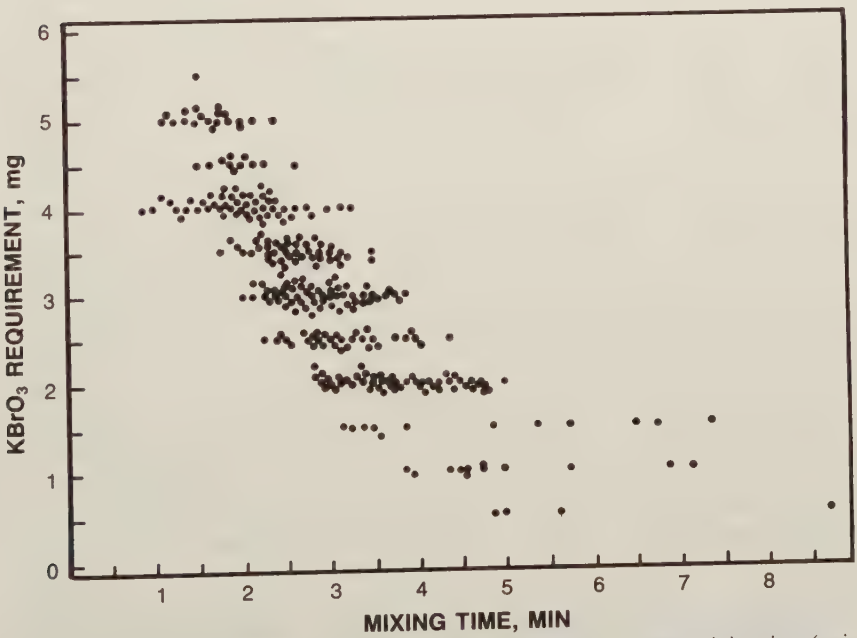

Fig. 10–18. Relation between oxidation ($KBrO_3$) requirement and dough mixing time (point of minimum mobility) of hard winter wheat flour composites representing a narrow range in protein content and a wide range in other breadmaking properties.

10–2.7.7.3 Dough Handling Properties vs. Mixing Requirement. A reasonably accurate index of relative dough stability, elasticity, buckiness, and extensibility can be obtained from mixogram mixing time (time to peak). For example, a dough having a short mixing time of 1.5 min almost invariably will be less stable, less elastic, and more extensible than a dough having a longer mixing time of 2.5 to 3 min. In general, as mixing time increases, dough extensibility decreases and dough stability and elasticity increase. As dough mixing time increases beyond about 4 or 5 min, however, the usually normal and desirable degree of elasticity and extensibility disappears and the doughs become increasingly bucky. In addition, long mixing times often complicate the baking schedule and increase production costs. Thus, doughs having extremely short mixing times usually have a predominance of extensibility and insufficient elasticity for a stable dough; whereas doughs having unusually long mixing times generally have insufficient extensibility for desirably elastic properties. Very short as well as extremely long mixing times, therefore, are undesirable properties.

10–2.7.7.4 Water Absorption vs. Protein Content, Cultivar, and Mixing Requirement. Working (or "as received") flour absorption is a function of flour protein content, cultivar, flour moisture, and environment. Mixogram or baking absorption is determined with the aid of the data illustrated in Fig. 10–6. The regression line to be used for an unknown is estimated from the regression lines of the parents. If the parents are not known, the approximate mean regression line represented by 'Kharkof' (Kk) or 'Tenmarq' (Tm) is employed. Thereafter, estimated absorption on a 14% moisture basis is readily adjusted for flour moisture content to give the "as received" absorption for the mixogram or for breadmaking.

When a number of sister progenies are involved, the composite effect of cultivar and environment can be determined accurately after a few grams of each are composited to give about 30 g of flour for preliminary mixograms to ascertain the suitability of the estimated absorption level. Thereafter, the regression line representing the adjusted mean absorption of the sister progenies is selected and applied to each sister. In that way, selected absorptions seldom are far enough off to prevent the reliable determination of mixogram mixing properties.

Short-mixing cultivars have absorptions that may be either above or below the average. It is highly significant, however, that wheat cultivars with medium to medium- long mixing times almost invariably have above-average water absorptions. Thus, approximate water absorption level can be predicted from the mixing requirement, particularly when only the relatively strong progenies with medium to medium-long times are selected.

The absorption–protein regression lines for breadmaking flours (Fig. 10–6) were obtained when 4% nonfat dry milk (NFDM) was in the formula. Those values are correct or 1% slack for mixogram absorptions.

When running flour-water mixograms, the absence of shortening increases mixogram absorption 1.5 to 2.0%. In breadmaking, the 3.5 to 5.5% of yeast (about 70% moisture) contributes 0.5 to 1.0% water that is not considered in breadmaking absorption. That 0.5 to 1.0% of water plus 1.5 to 2.0% for the omission of shortening equals 2.0 to 3.0%, which approximately equals the 3.0% of water required by 4% NFDM in the breadmaking formula. When 4% NFDM is omitted in the breadmaking formula, bake absorption will be 3.0% less than the values in Fig. 10–6, and mixogram absorption will be 2.0 to 3.0% greater than bake absorption.

10–2.7.7.5 Loaf Volume vs. Mixing Requirement. Loaf volumes of more than 300 samples, representing a wide range of wheat cultivars harvested throughout the Southern and Central Great Plains in 1961 and 1962, were corrected to 13% protein. Loaf volume at the 13% protein level increases as mixing time increases from seven-eighths to about 3 min (Fig. 10–19). Beyond 3 min, loaf volume is approximately constant with increasing mixing time. The lowest loaf volumes for mixing times greater than 3 min are considered to be barely satisfactory. Most of the others, however, are very good to excellent. Thus, mixing time or requirement obtained from the mixogram is a reliable index of loaf volume

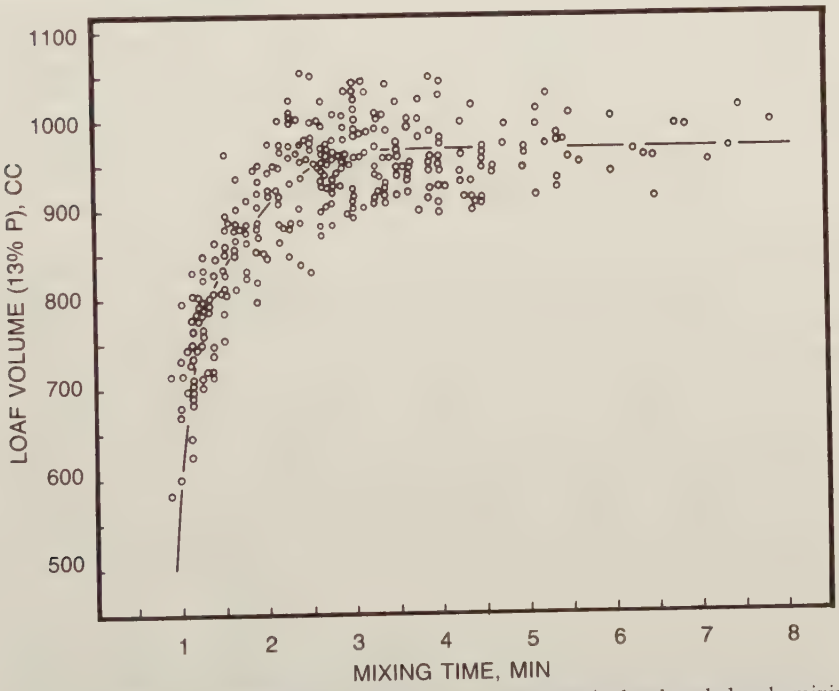

Fig. 10–19. Relation between loaf volume at the 13% protein level and dough mixing requirement (point of minimum mobility) of hard winter wheat flours representing a wide range in breadmaking properties. Samples with flour protein contents of about 11% and less were omitted because of their abnormally long mixing times.

potential or protein quality, when selecting cultivars that have mixing requirements of about 3 min or greater. Those data were corroborated by similar results for European wheats harvested at Manhattan, KS in 1977 (Finney et al., 1985).

10–2.7.7.6 Determination and Prediction of Functional Properties. The foregoing data and discussion demonstrate that physical dough properties (mixing requirement and mixing tolerance) are objectively determined from the mixogram, and that dough handling properties, water requirement, oxidation requirement, and loaf volume potential (on a constant protein basis) are predictable from mixogram mixing requirement. Those breadmaking properties are categorized in Table 10–2.

10–2.8 Contributions of Flour Components to Breadmaking Properties

Breadmaking, involving biochemical and physico-chemical systems, is an essential analytical test in the scheme of relating physical and biochemical properties of important wheat-flour fractions and components to functional properties. The only apparent way to bridge the gap between functional baking research and biochemical research on wheat and flour is by fractionation and reconstitution techniques. Normal functional properties of wheat fractions and components can be demonstrated only when each fraction is chemically and physically unaltered and is allowed to perform and interact singly and in various combinations with the other essential ingredients of a fermenting and optimum dough (Finney, 1954, 1978b, 1984; Finney et al., 1976). Fractions and components are considered to be unaltered when the functional properties of the reconstituted flour or dough are equal to those of the original flour.

10–2.8.1 Early Studies

The success of fractionation and reconstitution techniques in bridging the two areas of research and in identifying the wheat-flour components responsible for specific functional properties was reviewed by Hoseney and Finney (1971) and Finney (1971). Those studies yielded strong evidence that the glutenin proteins were responsible for mixing requirement and the gliadin proteins for loaf volume potential of bread wheat flours.

The nongluten proteins (salt-soluble globulins and water-soluble albumins and glycoproteins) are essential, because they greatly enhance the functionality of the gluten proteins (Finney, 1943; Hoseney et al., 1969).

10–2.8.2 Recent Studies

Goforth and Finney (1976) physically separated glutenin from gliadin by ultracentrifuging the acid-soluble gluten at 435 000 $\times$ *g*. Properties of bread made from the preliminary reconstitutions of the wet protein fractions indicated that the gliadin and glutenin fractions were 100% functional (unpublished data). Based on that work, Jones et al. (1983) found

Table 10–2. Categorization of mixing requirement and tolerance (physical dough properties) and related properties predictable from mixogram mixing requirement.

Mixogram		Physical dough properties	Properties predictable from mixogram mixing time			
Mixing time	Mixing tolerance		Dough handling	Water requirement	Bromate requirement	Loaf volume
min						
5¼–7¼ (long)	≦ Good	Very strong to bucky		≧ Good	Small	≧ Good
3¾–4¾ (medium-long)	≦ Good	Strong	Good	≧ Good	Medium small	≧ Good
2¾–3¼ (medium)	Fair to good	Mellow to medium strong	Fair to good	Good	Medium	≧ Good
1¾–2¼ (short)	Poor to fair	Weak to mellow	Poor to fair	Poor to good	Medium large	Poor to good
1 –1½ (very short)	Very poor to poor	Very weak to weak	Very poor to poor	Very poor to fair	Large	Very poor to fair

that the corresponding fractions of acid-solubilized glutens of good and poor quality wheat flours sedimented at different rates. They determined the time at 100 000 × *g* required to sediment the 11 to 15% high-molecular-weight protein fraction (pellet) and the time at 435 000 × *g* to sediment an amount of gel protein (35 to 31%), so that about 54% of the acid-solubilized gluten protein would remain in the combined viscous layer and supernatant protein fractions of both good and poor quality bread wheats.

The gel, viscous layer, and supernatant gluten proteins sedimented at 435 000 × *g* are essentially the same proteins that were unseparated in the 100-5S fraction described in the reviews of Hoseney and Finney (1971) and Finney (1971). In subsequent studies (Finney et al., 1982), good quality (RBS-76) and poor quality (76-412) hard winter wheat flours were fractionated into crude gluten and starch plus water-soluble fractions. Gluten proteins, solubilized in 0.0045 to 0.005 *N* lactic acid, were sedimented by ultracentrifugation into a pellet (high molecular weight, relatively insoluble glutenins), a gel (low molecular weight, relatively soluble glutenins), a viscous layer (high molecular weight, soluble gliadins), and a supernatant (low molecular weight, soluble gliadins).

The corresponding gel and viscous layer plus supernatant fractions of the good and poor quality flours were interchanged singly in reconstituted flours containing the starch plus water-soluble fraction and baked into bread (10 g of flour). The gel glutenin proteins of the acid-soluble gluten proteins controlled mixing requirement and baking absorption, and the viscous layer and supernatant gliadin proteins controlled loaf volume and crumb grain.

10-2.8.2.1 Sedimentation Properties of Protein Fractions. Sedimentation rates and physical properties of the different protein fractions varied greatly within a quality level, and the sedimentation rate of a given protein fraction varied materially between the two quality levels.

The relative ease with which the high-molecular-weight pellet glutenins sedimented after only 35 to 120 min at only 100 000 × *g* suggests that they are relatively free compared to the low-molecular-weight gel glutenins that sedimented after an additional 6 to 10 h at the high relative centrifugal force of 435 000 × *g*. The gel glutenins appear to be relatively tenaciously interacted or bound to the gliadin proteins. Hoseney et al. (1970) demonstrated that essentially all natively bound lipids of wheat flour were polar lipids and were associated with the high-molecular-weight pellet proteins. The extent to which the bound polar lipids interacted with the pellet proteins, both intra- and intermolecularly to produce extremely high-molecular-weight aggregates, may render them relatively nonreactive with the gel glutenin and gliadin proteins, so that the pellet glutenin proteins are relatively free to sediment at relatively low centrifugal forces.

10-2.8.2.2 Molecular Interactions Affect Sedimentation Proper-

ties. When flour is wetted and mixed into a dough or when gluten is forming, all of the free polar and about half of the free nonpolar lipids become bound (no longer extractable in petroleum ether) and are presumed to form lipoprotein complexes with the glutenin fraction of gluten protein (Olcott and Mecham, 1947). The ease of sedimenting the pellet glutenins indicates that they are not involved in the formation of additional lipoprotein complexes and that the free lipids become bound, probably by interacting with reactive gel glutenin and reactive gliadin proteins. Similarly, when the dough is formed, reactive gel glutenins probably interact with reactive gliadins. Thereby, the gel glutenin proteins become bound. When the centrifugation forces are greater than the protein interaction forces but less than the molecular forces that keep the relatively small gliadin proteins in solution, then the gel glutenins sediment.

10–2.8.2.3 SDS-PAGE Patterns of Protein Fractions. When progressing from the sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) patterns of the supernatant to the gel protein fractions, densities of the rapidly moving bands (small proteins) decreased, and number and densities of the slowly moving bands (large proteins) increased (Finney et al., 1982).

In SDS-PAGE studies, many types of bonds are broken, so that many component parts of the original functional protein fraction are visible. Those parts likely are irreversibly nonfunctional and may be common to two or more protein fractions that have different physical and functional properties. Thus, the repetition of bands is not necessarily an index of a mixture, impurity, or similarity of proteins.

10–2.8.2.4 Probable Relationships Between and Within Functional Properties and Protein Fractions. A cultivar with a very short (very poor) mixing requirement almost invariably has a low (poor) loaf volume potential. Similarly, a cultivar with a medium (good) to medium-long (very good) mixing requirement almost invariably has a good to very good (relatively high) loaf volume potential (Finney and Yamazaki, 1967). Because loaf volume is a function of gliadin quality, and mixing requirement is a function of glutenin quality, good and poor quality glutenins are related to or associated with good and poor quality gliadins, respectively. Those relationships are diagrammed in Fig. 10–20.

Considerable cytogenetic research since 1975 (Morris, 1975–1984) has shown that genes for both gliadin and glutenin are located on chromosomes 1A, 1A short, 1B, 1B short, 1D, 1D short, 6A, 6B, and probably others. Those data indicate that a direct relationship between the qualities of gliadin and glutenin would be anticipated and, together with the other direct relationships between glutenin quality and mixing requirement and between gliadin quality and loaf volume, supports the indirect relationships indicated by the broken lines in Fig. 10–20.

The data in Fig. 10–19 (p. 703) show that loaf volume increased as

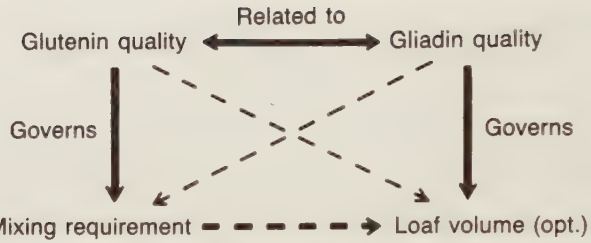

Fig. 10–20. Diagram of likely direct and indirect relationships between glutenin quality, gliadin quality, and the functional properties, mixing requirement and loaf volume (optimum). Broken lines indicate indirect relationships. The wider the line, the stronger the relationship. Also (not shown), glutenin quality governs mixing tolerance and dough absorption (attributable to flour proteins). Oxidation requirement and dough stability are strongly related indirectly to mixing requirement.

mixing requirement increased from less than 1 to about 3 min. Thereafter, loaf volume remained constant for mixing times greater than about 3 min. Those data and similar correlation studies by others have been interpreted by some as evidence that the glutenins control loaf volume. The significant correlation of mixing time and loaf volume is attributable to the probable relationship of glutenin and gliadin quality. One variable being correlated to another does not mean that the one is directly related to or governed by the other. The reconstituted flours in which glutenin or gliadin protein fractions of good and poor quality wheat flours were interchanged are direct evidence of the role of each protein fraction in breadmaking.

10–2.8.2.5 Study Protein Fractions Before Disassembling Them. Functional gluten protein fractions must be studied before they are disassembled during physico-chemical, biochemical, or instrumental analyses, so that PAGE and other biochemical properties can be related to them. The less complex the functional protein fraction, the more specific is the scientific information on that fraction. Thus, studies on functional glutenin fractions and gliadin fractions are more revealing than those on the total functional glutenins or gliadins. Further fractionation of the pellet and gel glutenins and the viscous layer and supernatant gliadins into less complex functional fractions should be additionally revealing, and should allow PAGE and other biochemical properties to be more specifically related to physico-chemical and functional (breadmaking) properties.

10–3 QUALITY OF SOFT WHEAT

10–3.1 Milling Properties

10–3.1.1 Kernel Hardness

Soft wheats differ from hard wheats in kernel hardness, a basic genetic characteristic inherited simply and directly. When ground or milled, soft

wheat fractures into significantly smaller particles than hard wheat, reflected in the greater quantity of break flour in milling (Yamazaki and Donelson, 1983). Break flour is the portion of the kernel endosperm of flour fineness obtained without crushing or reduction in the milling operation. Soft wheat cultivars exhibit a wide range in kernel texture, but there is a distinct difference in average flour particle size between the hardest soft wheat and hard wheats, such that a relatively simple grinding test can classify wheat properly.

10-3.1.1.1 Protein Content and Kernel Hardness. Low protein soft wheat is opaque or mealy, but at higher protein the grain is or can be translucent or vitreous. This change in appearance within a cultivar does not change its kernel hardness significantly. In other words, a soft wheat cultivar mills like a soft wheat whether it is low or high in protein content. Vitreosity in soft wheat has been a cause of misapprehension on the part of a number of workers who have been led to believe that all vitreous grain has hard wheat milling and baking properties. This belief apparently arose because in the past almost all vitreous grains were hard wheat cultivars and soft wheat cultivars were usually grown in areas in which low protein, and hence mealy kernels, was the rule.

10-3.1.2 Flour Yield

An important economic property of wheat is flour yield, apart from the suitability of its flour for baking. Among soft wheats, flour yield has been shown to be a cultivar trait (Yamazaki and Andrews, 1982a), rendering it amenable to breeding in a manner similar to kernel hardness. Under closely controlled experimental milling conditions, cultivar flour yield has been shown to range from a high of 79% to a low of 72% on a total products basis.

Flour yield potential is better expressed when the experimental milling technique is optimized for each wheat being tested, rather than subjecting grains differing in milling response to a uniform procedure. Mill optimizing is best suited for evaluating wheat, since commercial mills adjust milling conditions to maximize yield from the grist.

10-3.1.3 Test Weight (Weight per Bushel)

Test weight of normal (unshriveled and undamaged) soft wheat grain is the combination of two factors: the density of the kernel itself and the random volume occupied by the grain (packing efficiency). Kernel density reflects the environment in which the grain was grown and is dependent on the volume of air in the grain as well as protein content to some extent, which also affects grain appearance. Low protein grain (mealy in appearance) has more or larger air pockets than those of relatively high protein kernels (vitreous in appearance), which may have no air pockets at all. Presumably, in the low protein dry wheat there is insufficient protoplasmic (protein) material to fill the interstices between starch granules

in the cells. It has been found, however, that packing efficiency in soft wheat is a cultivar or heritable trait (Yamazaki and Briggle, 1969) associated with grain shape. Thus, grain that closely resembles a regular geometric figure, such as a prolate spheroid, has a greater efficiency than an irregular one. Grain of certain cultivars have humps, lateral depressions, or wrinkles on the dorsal parts of kernels, which lower packing efficiency. The authors found the cultivar Yorkstar to be distinctly lower in packing efficiency than 'Genesee', which in turn was lower than 'Knox 62'.

Inherent tendencies for low test weight among wheat classes and subclasses are recognized by the USDA Federal Grain Inspection Service (1977), which grades club wheat as No. 1 at test weight of 58 lb/bu or greater while other wheat of the same grade (other than hard red spring) must have test weight of 60 lb/bu or greater. Club wheat, a soft textured subclass of white wheat and grown in the Pacific Northwest, is deformed as the direct result of its compact head formation and is therefore low in packing efficiency, hence low in test weight. Weight per bushel has often been related to flour yield in milling, but low weight per bushel due to low inherent packing efficiency does not necessarily result in low flour yield, and in fact, some of the highest flour yields are for club wheats.

10-3.1.3.1 Loss in Test Weight. Test weight decreases with kernel deformation, especially by shriveling, and in these cases, there is an obvious increase in ratio of bran to endosperm and concomitant yield loss. Damaged or weathered kernels, foreign material, and high moisture content also lower test weight. Test weight is a factor determining market grade, and a discount is usually applied to low test weight grain. Milling studies conducted on Pacific Northwest soft wheat have shown a decrease in yield of about 1% as well as an increase in flour ash content of about 0.025% for each 1-lb decrease in test weight within a test weight range from 64 to about 30 lb/bu for the grains tested.

10-3.1.4 Flowability of Flour During Milling

In commercial milling, flour streams are conveyed through ducts to rolls, screens, and other ducts, mostly by gravity; hence, flowability is an important wheat property. Much of the fineness of soft wheat is attributed to the presence of free starch granules, which contribute to poor flow properties. In extreme cases, this difficulty can result in choke-up or bridging that plugs ducts. Flour flowability appears to be directly related to kernel softness, a trait susceptible to breeding; thus, it seems probable that flowability can likewise be controlled.

10-3.1.5 Protein Conversion in Milling

When wheat of a given protein content is milled to flour, the resulting flour protein content is normally lower than that of the grain, the magnitude of the difference being a function of both the milling procedure

and flour yield. Usually the difference decreases with increased flour extraction. Protein conversion is important in hard wheat milling, where high protein content is sought. In soft wheat milling, high flour protein content is usually not an objective. Instead, low flour protein content and high flour yield are usually desired.

10–3.2 Prerequisits for Good Milling Quality

A soft wheat of good milling quality should fracture into particles of significantly smaller median diameter than hard wheats, but not be so soft as to cause poor flowability through ducts or inhibit proper bolting (sieving). It should be low to medium-low in protein content and should have high weight per bushel (depending on class). High flour yield, normal flour ash content, and minimum power requirement are important prerequisits for good milling quality.

10–3.3 Baking and Other Processing Properties

Soft wheat flour is used commercially in the U.S. domestic market for the production of cookies, cakes, saltines, wafers, and similar products collectively termed *flour confectionary goods.* The diversity in flour end-use and paucity of definitive information regarding the chemistry, physics, and biochemistry of baking of the various products complicate consideration of soft wheat baking properties and product quality.

Much (85% or more) of soft wheat grown in the Pacific Northwest is exported to the Asian and African markets, where it is used in the production of baked and other goods significantly different from those in the domestic U.S. industry. For importing nations, popular products such as flat bread, noodles, and steamed products may require wheat and flour processing properties different from those for confectionary goods.

Soft wheat products may be described by classifying them into three broad groups: chemically leavened products exemplified by cookies, cakes, and wafers; secondly, yeast leavened products such as saltines, pretzels, and flat breads; and thirdly, nonbaked products, among which are noodles and batter coatings for fried foods.

10–3.3.1 Chemically Leavened Baked Products

Most chemically leavened products are rich in sugar and fats. Ammonium bicarbonate or baking powder (usually a combination of sodium bicarbonate and an acid-producing compound such as a phosphate) is the normal leavening, and the CO_2 generated during baking provides the gas required for the leavening action. In dough or batter mixing, an important step in processing, full gluten development is normally avoided since a *short* product (one which emphasizes tenderness) is desired. Product tenderness is the quality goal for most flour confectionary goods, and although the concept is ill-defined from the functional property stand-

point, commercial processors feel that for most products tenderness is attained most readily through the use of soft wheat flour and with a minimum of gluten development.

Baking quality of soft wheat cultivars and breeding lines for chemically leavened products may be expressed in terms of the relation between water absorption requirement of flour and the spread (increase in diameter) of test cookies baked under specified conditions. While a popular belief exists that coarsely granulated flour is higher in water absorption than finely divided flour, such is not always the case. For example, although club wheat flours are relatively granular, they are among the lowest in water absorption and produce correspondingly large-spreading test cookies.

Soft wheat baking quality may also be expressed in terms of the association between flour particle size and cake volume using a specific test baking formulation and procedure (Yamazaki and Donelson, 1972a). The precise nature of this association has not been established. However, it appears possible that high flour specific surface contributes to effective reaction between flour and chlorine gas, which contributes significantly to improved cake quality.

10-3.3.2 Yeast Leavened Baked Products

Processing of yeast leavened products, involving fermentation and other biological (bacterial) activities, differs widely from those for chemically leavened goods. The functional properties of the flour are more important in yeast leavened than in chemically leavened products, because only small quantities of sugar and fats are included in yeast leavened formulations. As in breadmaking, the proteins are the prime components of interest in the processing of saltines and pretzels. However, the preference by commercial saltine producers for soft wheat flour over hard wheat flour, based on detected differences in product tenderness, implies a class difference in response to processing.

Flour for flat bread may range from conventional white to near whole wheat, absorption from 45 to 85% (flour basis), fermentation time from only a few minutes to several hours, and baking time from 1 to 15 min at oven temperature ranging from about 175 to 550°C. Bread quality as gauged by consumer acceptance is associated with light crust and crumb color and with crust flavor. Flours with short mixing requirements and with weak (mellow) gluten properties are considered desirable for traditional flat breadmaking, because they yield bread that is not tough or excessively chewy (Faridi and Rubenthaler, 1983b).

10-3.3.3 Nonbaked Products

Noodles comprise a major nonbaked product of soft wheat, accounting for about 25% of the total flour consumption in the Orient (Nagao et al., 1976). Most noodles in Japan are made by cutting sheeted dough, rather than by stretching or extruding. The flour required for high quality

noodles has gluten properties intermediate between those required for bread and for cookies; it has white color, fine granulation, intermediate water absorption requirement, rapid water uptake (short mixing time), and low enzymatic activity.

Other nonbaked products include batter coatings for deep-fat fried foods such as seafood, poultry, and certain vegetables. Flour with low protein content and soft gluten quality, together with low amylase activity, is preferred. Cake donuts are leavened with baking powder but are fried rather than baked. Flour requirements are complex, involving the blending of soft and hard wheat flours and soy flour.

10–3.4 Prerequisites for Good Processing Quality

Simply stated, the prerequisites for good soft wheat flour quality are the conformity of such flours to the baking performance of widely grown commercial cultivars. It is generally agreed in the industry that such cultivars are satisfactory. Thus, a flour of good quality should have a low to medium-low protein content and a low water absorption, and should bake large-diameter test cookies and large-volume cakes, both with good external appearance and satisfactory internal grain structure. It should also bake good quality saltines and flat breads, as well as make good nonbaked products such as noodles.

The release and wide distribution of new cultivars with baking responses closely resembling those of present cultivars should bring about minimal quality disruption when mixed in the market, and can thus help maintain the high quality of presently grown soft wheats.

10–3.5 Milling Methods

10–3.5.1 Macromilling

Rigorous evaluation of soft wheat for milling quality may be carried out on moderate size (2-kg) samples using a modified Allis-Chalmers laboratory mill (Yamazaki and Andrews, 1982a; Fig. 10–21). The procedure has been found to give replicable yields of low-ash straight-grade flour, thereby making it possible to identify cultivars and breeding lines with high yield potential, a heritable trait. It also enables the determination of the endosperm separation index, a measure of ease of separation of bran and endosperm, also apparently a heritable grain attribute highly correlated with cultivaral flour yield potential.

The milling is preceded by a series of wheat-cleaning operations to remove shriveled grain, as well as foreign material, chaff, and similar non-flour-producing substances. The grain is then conditioned by the addition of sufficient water to bring its moisture content to an appropriate milling level. These steps help to assure that extraneous variables are minimized and that optimum milling conditions prevail.

Another experimental mill used in cereal laboratories to produce flour

Fig. 10–21. A 4-stand Allis-Chalmers laboratory experimental flour mill modified for cultivar evaluation and for research.

in moderate quantity is the Buhler mill, an automatic mill also designed to accommodate about 2 kg of grain (Shellenberger and Ward, 1957). In addition to flour yield, other economically important milling factors have been incorporated into a composite formula to provide a milling score that is an evaluation of overall milling quality (Seeborg, 1951). These additional factors include rate of milling, wheat moisture level, patent flour yield, and flour ash content, all weighted in a manner considered by commercial interests to indicate applicability to milling quality.

For laboratory-scale quantities larger than about 5 kg up to hundreds of kilograms, milling can be carried out in a MIAG Multomat mill (Fig. 10–22). This is a fully automated mill with many features rendering great flexibility in feed rate, roll distance, and screen arrangement. It is suitable for assessing the yield potential of large samples of grain, as well as for producing quantities of flour for distribution among collaborators in evaluating flour baking quality and for research.

10-3.5.2 Micromilling

It is often advantageous to be able to appraise the flour yield potential of breeding lines early in a program, when the quantity of grain for testing is severely limited. A procedure using a modified Brabender Jr. mill for experimental soft wheat lines (Yamazaki and Andrews, 1982b) yields data that correlate significantly with those obtained with the Allis-Chalmers mill above. The mill requires only 20 g of unconditioned grain per test.

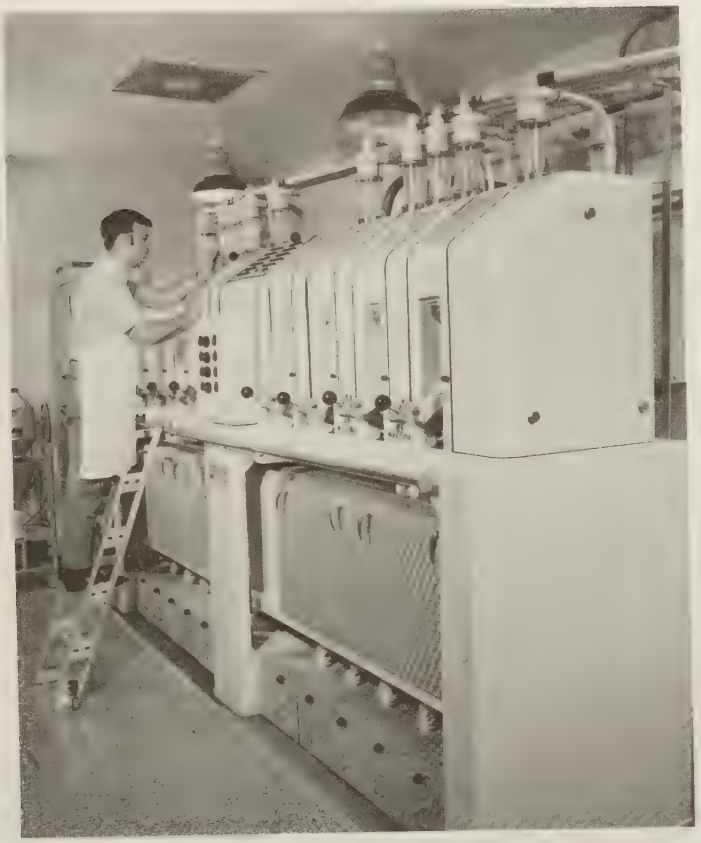

Fig. 10–22. The MIAG Multomat mill, a fully automated laboratory 3-break and 5-reduction experimental flour mill for wheat samples larger than about 5 kg.

Since moisture content influences yield, an adjustment in yield data is made for grain moisture content.

A number of other small-scale soft wheat milling methods have been developed to determine flour yield potential, or simply to recover flour for baking quality tests. These have been described by Finney and Yamazaki (1946), Shoup et al. (1957), and Kemp et al. (1981). Jeffers and Rubenthaler (1977) modified a Brabender Quadrumat Sr. mill to obtain improved flour yield data that correlated highly with Buhler milling score. It is not known whether data from other small-scale milling methods have been compared directly with those from larger and more sophisticated equipment.

10–3.6 Baking and Other Processing Methods

10–3.6.1 The Cookie Test

The cookie baking test, used in a number of government and private quality laboratories, is a modification of the official American Association

of Cereal Chemists test (AACC, 1983) and was first described by Finney et al. (1950). This is a micro or small-scale test requiring only 40 g of untreated flour. Two cookies are baked from a dough mix. The principal criterion of quality is the increase in diameter of the product (Fig. 10–23). A flour from which the cookies are of larger diameter than those of another is said to be superior in its response to the test (Fig. 10–24). Research has shown that the increase in cookie diameter is highly correlated inversely with the water absorption requirement of the flour and to a lesser extent with protein content. Both cookie quality and water absorption capacity are heritable traits. Although their absolute levels are influenced to some extent by environment (and season or crop year appear to be more significant than location), the relative rankings of cultivars and lines do not seem to vary to any appreciable extent.

10–3.6.2 The Layer Cake Test

A second baking test used in several laboratories is the white layer cake test (AACC, 1983), termed *high ratio* because of the relatively large quantity of sugar in the formulation (Yamazaki, 1970). The flour used in this test is usually of short extraction (50%, wheat basis), pin milled to reduce average particle size (increase specific surface), and treated with chlorine gas to a given pH. The basis for evaluation is cake volume (Fig. 10–25 and 10–26). Because of the need for a special milling to obtain patent flour and the relatively large quantity of flour required per bake

Fig. 10–23. A device for measuring cookie diameter. An average sum of two cookies is obtained from four measurements. After the first measurement, cookies are rotated approximately 45, 90, and finally 135° for three additional measurements.

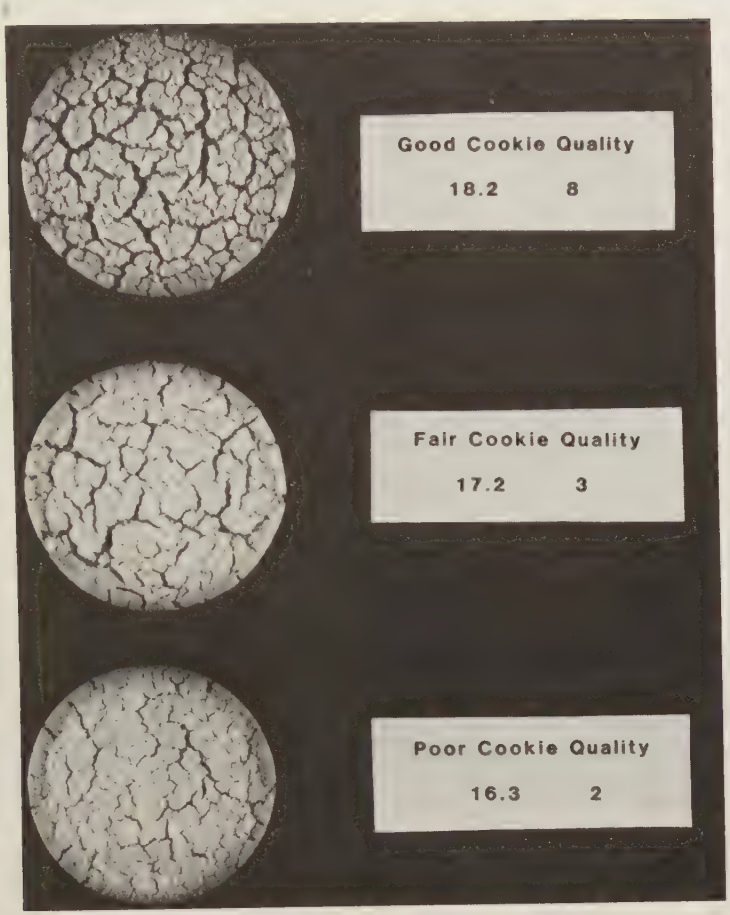

Fig. 10–24. Test cookie from a flour of good cookie quality potential (*top*), a cookie from a lesser quality soft wheat flour (*center*), and a cookie from a typical hard wheat flour (*bottom*). Numbers on labels are sums of the diameters of two cookies (in centimeters).

(110 g), the cake test is not applied in an evaluation program until fairly late in cultivar development. However, some measure of cake quality potential can be obtained without baking, because studies have shown an association between flour fineness and cake volume potential (Yamazaki and Donelson, 1972a). Flour fineness closely parallels kernel hardness, which can be measured by the PSI test when applied to only a few grams of grain early in breeding line development. (The PSI is discussed in section 10–3.7.1, below.)

10–3.6.3 Flat Bread Test

An important product of soft wheat in the Middle East and Indian subcontinent is flat bread. Innumerable types are popular, differing in taste, texture, and appearance but sharing a common freshly baked flavor

Fig. 10–25. Rapeseed displacement apparatus for measuring cake volume. Measurements are made on cooled cakes that have been floured to prevent seed adhesion. Volume is determined by weighing displaced seed after calibration of its bulk density.

(Fig. 10–27 and 10–28). The formulation is simple and includes only flour, water, salt, and a low level of leavening (yeast or sour-starter), which produces a low calorie bread. Baking flat breads, although carried on for millenia, remains more an art than a science, with only recent investments in automated bakeries. The technical and processing properties of a number of Persian-style flat breads were described by Faridi and Finney (1980) and by Rubenthaler and Faridi (1981).

10–3.6.4 Sponge Cake and Noodle Tests

The large export market demands for Pacific Northwest soft white wheats have necessitated assessing the suitability of such wheats for products other than cookies and layer cakes. Tests found to be most useful to measure wheat quality for the Far Eastern market are those for sponge cake (Fig. 10–29) and noodles (Nagao et al., 1976, 1977). Procedures described by these authors and their modifications are used throughout Far Eastern milling and baking industries as well as in wheat breeding

Fig. 10–26. Section of cake baked from wheat flour with good cake potential (*top*) and from one with lesser potential (*bottom*). Numbers on labels are cake volumes (in cc).

programs in the Pacific Northwest. A part of product quality evaluation is objective in nature, such as measuring cake volume or noodle yield, but a significant segment of the testing program is subjective, such as scores for moistness, tenderness, softness, and eating quality, all of which require experience and acquired skills for quantifying differences. Sponge cake score is negatively correlated with flour protein content (Fig. 10–30), as protein influences cake volume and crumb properties (Noguchi, 1978). As in the layer cake test, these tests require relatively large quantities of flour, 100 and 500 g for the sponge cake and noodle tests, respectively. To date, no small-scale quick physico-chemical methods have been developed to assess either sponge cake or noodle quality potential, either in early generation breeding lines or in market channels.

10–3.7 Methods to Predict Functional Properties

10–3.7.1 Particle Size Index

Kernel hardness can be tested for in cultivars and breeding lines by grinding wheat and sifting the resultant meal under specified conditions

Fig. 10–27. Egyptian balady (pocket or pita) breads baked from 86% extraction soft white wheat flour.

(Fig. 10–31). Soft wheat yields a greater quantity of material passing through the sieve than a hard wheat. A greater range of kernel softness exists among soft wheat than for hard wheat, and there is usually a clear and distinct difference between hard and soft wheats in PSI, the percent of wheat passing through a sieve (Yamazaki and Donelson, 1983). Grain moisture content affects PSI and thus should be taken into account in conducting the test (Fig. 10–32). Although cultivars may differ in PSI, protein content within a cultivar does not appear to affect PSI significantly. Particle Size Index is also directly related to cultivar cake quality potential (Yamazaki and Donelson, 1972a).

10–3.7.2 Alkaline Water Retention Capacity

The alkaline water retention test measures the ability of a flour to hydrate in a dilute solution of sodium bicarbonate and retain the solution against centrifugal force (Yamazaki, 1953). Results of the tests have been found to correlate significantly inversely with cookie quality as determined by the cookie baking test, and a microversion of this physicochemical test has thus been applied to an early generation screening evaluation program (Yamazaki and Donelson, 1972b; Fig. 10–33 and 10–34).

Fig. 10–28. Persian style lahvosh breads baked from 82% extraction soft white wheat flour.

10–3.7.3 Protein Content

Since it is generally agreed in the domestic U.S. soft wheat industry that low flour protein content is desired in order to maximize product tenderness, one of the objectives in quality evaluation is to promote the development of cultivars inherently low in protein. A recent approach to breeding, however, is to seek experimental lines that break the traditional protein-product performance relationship by having higher protein but performing as those wheats with lower protein content. This approach may have merit for regions exporting soft wheat to nations where protein is needed in the diet and where wheat represents a large portion of food intake. Testing grain for protein content is therefore a basic procedure, generally carried out using the Kjeldahl methods or near infrared reflectance spectroscopy (discussed in section 10–2.7.1).

10–3.7.4 Acid Viscosity

The acid viscosity test in soft wheat is an extension of its application to hard wheat for bread quality. There is some question in the industry as to just how well results of the test are related to soft wheat quality, although it appears to find some application in specifying flour for the saltine industry. The viscosity value, a measure of the extent of protein

Fig. 10–29. Sponge cakes baked from 60% extraction flours of composite samples of soft wheats from different parts of the world (Nagao et al., 1977).

swelling in a lactic acid medium, is influenced by quantity of protein as well as by soluble ash. These variables should thus be minimized or adjusted for when the test is used for intercultivaral comparisons. While data are not presently available, it is possible that viscosity may be related in some way to product tenderness. For most soft wheat applications, it appears that low adjusted viscosity value is desired in cultivars, but in some cases, such as saltines, optimum values may be higher.

10–3.7.5 Mixograph

The mixograph, used with considerable success in the evaluation of hard (bread) wheat breadmaking properties (Finney and Shogren, 1972), has been applied with inconclusive results in the evaluation of soft wheat flour for North African bread (Faridi and Rubenthaler, 1983a). Although more research appears desirable to clarify the relationship between mixograph data and North African bread quality, there appears to be a preference for soft wheat among consumers, presumably because of tender texture imparted to the product.

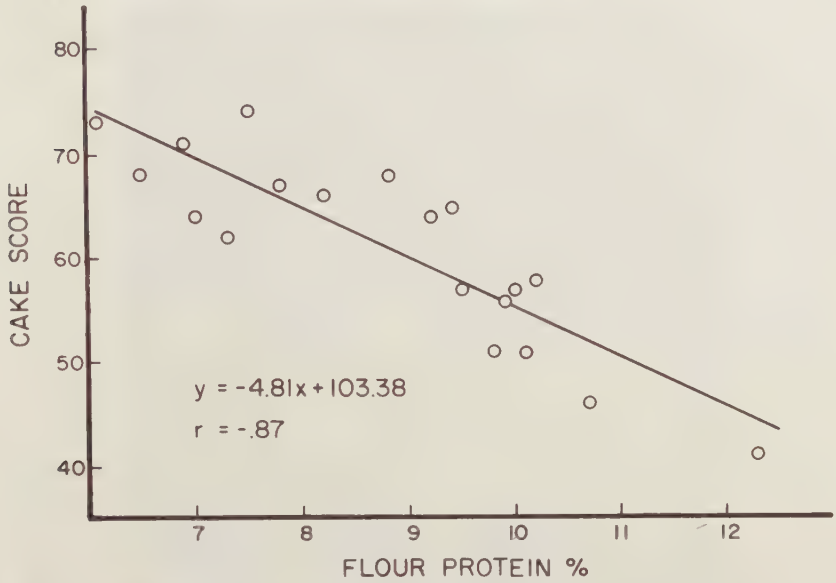

Fig. 10–30. Regression for sponge cake score vs. flour protein content, selected soft white winter cultivars harvested in 1974 to 1976 (Noguchi, 1978).

Fig. 10–31. Cleaning out grinding chamber following the grinding of grain for the Particle Size Index test.

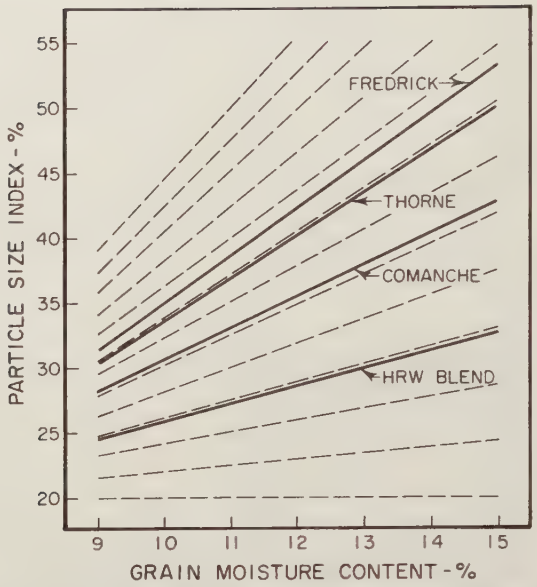

Fig. 10–32. Idealized family of regression lines for Particle Size Index vs. wheat grain moisture content within a sample (*broken lines*). Data for four wheat samples are also shown (*solid lines*). Note that the slopes vary with the degree of inherent softness of the grain (Yamazaki and Donelson, 1983).

10–3.7.6 Farinograph

The farinograph, an instrument used to determine the absorption and mixing requirements of flour, pricipally for bread purposes, is also useful in determining flour absorption as related to cookie potential. It has also been applied to evaluate flour for specific soft wheat products in certain private laboratories, but has not been extensively used in breeding programs, possibly because of the need for larger size samples than for most other tests for early generation evaluation and because of the relatively high cost of the apparatus.

10–3.8 Contributions of Flour Fractions to Processing Properties

10–3.8.1 Cookie-Baking Properties

The relation between flour water absorption requirement and quality was investigated by Yamazaki (1954) and by Yamazaki and Donelson (1976, 1977). The latter studies, carried out using the techniques of flour fractionation and reconstitution, indicated that much of the inherent differences in absorption and therefore in cookie quality could be attributed to the starch tailings fraction, a heterogeneous component consisting of hydrophilic substances such as hemicelluloses and damaged starch. The quantitative and qualitative differences in these compounds ap-

Fig. 10–33. Adding dilute sodium bicarbonate solution to flour in the micro alkaline water retention capacity (AWRC) test.

peared to be due to inherited traits and to the variable response of cultivars to milling.

The role of flour lipids in cookie quality was clarified by Clements and Donelson (1981), who found through thin layer chromatography that a lipid subfraction corresponding to digalactosyldiglyceride (and/or phosphatidylcholine) was required to produce well-formed normal cookies. Since those compounds have also been associated with the requirement for breadmaking, it would appear that they are involved in the mechanism of gas retention by the dough system. There did not appear to be class or cultivar differences in the nature of the compounds. The restoration of as little as one-half of the extracted flour lipids was sufficient to bring about normal cookie characteristics.

10–3.8.2 Cake-Baking Properties

Functionality of certain flour components in cake baking was reviewed by Yamazaki and Kissell (1978). Kissell and Yamazaki (1979) found that cake volume and batter stability increased as flour chlorination

Fig. 10–34. Preparing for centrifugation of hydrated flour suspension in the micro AWRC test. After centrifugation, the supernatant solution is decanted and the gel remaining in the tube is weighed by difference.

increased to optimum. Beyond optimum, restricted expansion limited volume, although batter stability continued to improve. They also noted that cake crumb texture changed from gummy without chlorination to dry with overbleached flour. At the optimal chlorination level, cakes were best described as moist to slightly dry.

Cake volume increase due to flour chlorination (Fig. 10–35) has been attributed to reactions which modify the functional properties of both the extracted free lipids and residual flour (Kissell et al., 1979). Aging of cake flour and heating of hexane-extracted flour lipids has also been shown to have volume-improving effects (Clements and Donelson, 1982a, 1982b). Gaines and Donelson (1981) compared the crumb textures of cakes baked from reconstituted flours in which the corresponding fractions of untreated and chlorinated flours were interchanged one at a time. They found a high degree of association between prime starch chlorination and decrease in crumb stickiness (or gumminess).

Reports of research on improvement in cake flour performance through treatments have tended to be at variance with each other or even to be contradictory. In their paper, Clements and Donelson (1982b) point out that the history of the flour may play a role in conflicting results. Storage conditions may have imposed varied oxidation effects. In addition, Kissell and Yamazaki (1979) stated that emulsified shortening may be a source of variable results. It is apparent that research on the

Fig. 10–35. Section of cake baked from pin-milled soft wheat patent grade flour treated with Cl_2 gas to optimum pH (*top*) and section of cake from same flour but without chlorination (*bottom*). Numbers on labels are cake volumes and cake scores (based on 100 for ideal cake).

mechanism of cake baking requires careful consideration of possible confounding factors that may influence conclusions.

10–4 QUALITY OF DURUM WHEAT

Durum wheat (*Triticum turgidum* L. var. *durum*) is grown throughout the world, although not as extensively as hard red winter (HRW) or hard red spring (HRS) wheat. In the USA, durum production for 1980 was about 23% of the total spring wheat crop and about 6% of the winter wheat crop, and 4.6% of the total U.S. wheat crop (USDA, 1982). A majority (70 to 80%) of the U.S. durum wheat is grown in North Dakota; some is grown in Montana and South Dakota and in the southwestern

USA, especially irrigated areas in Arizona and California. While durum is used for food in various ways throughout the world, its primary use in the USA is for pasta production, especially spaghetti, macaroni, and noodles.

10–4.1 Milling Properties

Commercial durum milling differs considerably from flour milling, because the desired end-product is semolina, not flour. Semolina is defined as the purified middlings of durum wheat that will pass through a No. 20 U.S. sieve, of which not more than 3% will pass through a No. 100 U.S. sieve. Other products obtained include durum granular that will pass through a No. 20 U.S. sieve but no more than 20% of which will pass through a No. 100 U.S. sieve. Durum flour is the purified endosperm of durum wheat that is ground fine enough to pass through a No. 100 U.S. sieve.

10–4.1.1 Kernel Characteristics

Durum wheat has a greater hardness than any of the other wheat classes. This is an advantage in the production of semolina, because the endosperm is less friable than that of softer wheats, allowing a higher yield of coarse-ground stock (semolina) and less durum flour.

In good quality durum, the test weight normally exceeds 60 lb/bu. The kernels are large, amber in color, and vitreous in appearance. Test weight, kernel size, and 1000 kernel weight can vary considerably, but they almost always exceed those of HRS and HRW wheat. Environment and heredity play roles in major kernel characteristics, as they do in other wheat.

When the durum plant is subjected to stresses and diseases, kernel disorders affecting quality can occur. *Helminthosporium sativum*, Pamm, King, and Bakke, known as blackpoint, causes a discoloration of the kernel. This can add undesirable black specks to semolina. The presence of starchy or yellowberry kernels affects milling quality. A starchy kernel, or the starchy part of a kernel, has a lower protein content than the vitreous portion. When milled, starchy kernels produce total milling yields similar to vitreous kernels, but less semolina and more flour are produced (Matsuo and Dexter, 1980a; Dexter and Matsuo, 1981). Shrunken kernels reduce total milling yield. (Sprouted kernels are discussed in section 10–4.3.4.)

10–4.1.2 Semolina and Flour Yield

Unless a mill is specifically producing durum flour for a special commodity such as noodles, semolina is the major product and flour is secondary. Commercial millers estimate that about 2.2 bu of durum wheat are required to obtain 100 lb of milled product; i.e., about 75% of the

kernel becomes milled product and the remaining 25% is considered feed. Of the milled product, 80 to 85% should be semolina. Semolina yield can be extended, but pigment content is affected, so that pasta color becomes browner and duller (Dexter and Matsuo, 1978a).

10-4.1.3 Protein and Ash

Durum protein content is controlled by fertilizer, environment, and heredity, but it generally is above 13% in whole grain. Semolina protein content generally is about one percentage point less than the whole wheat protein. A protein spread much greater than this is undesirable, because it is important to have the protein in the endosperm for its ultimate use in the food product.

Durum wheat and semolina ash values are higher than those of HRS wheat and flour. In the USA, ash is of little consequence in semolina quality evaluation, but in some countries, such as Italy, ash levels are specified by law.

10-4.2 Prerequisites for Good Milling Quality

The kernel characteristics previously listed all contribute to the milling properties of durum wheat (Matsuo and Dexter, 1980). Good kernel size and weight will generally mean more endosperm, and hardness will allow better control in grinding the endosperm to the proper particle size. Cultivars vary in how well the endosperm can be separated from the bran, and this is first observed in experimental milling. Diseased kernels such as blackpoint and shrunken kernels are undesirable, since semolina should be as free from specks as possible.

10-4.3 Pasta-Processing Properties

10-4.3.1 Protein Content and Gluten Strength

The basic ingredients in pasta production are water and semolina or flour. In the extrusion process, durum gluten probably is not fully developed, because the water absorption is extremely low (31–32% at 14% moisture basis, mb; Matsuo et al., 1978), yet sufficient protein is very necessary. Low-protein dough from semolina and water can be extruded successfully, but stretching may occur later in the drying process when the strands are placed over rods. In some cases, the strands will break under their own weight, especially where they bend over the rods. Generally, if the semolina protein is over 11 to 12% (14% mb) there is sufficient gluten strength to prevent breaking.

Gluten strength of semolina is generally low, as compared to flour milled from comparably grown HRS wheats. Durum breeders have been selecting for stronger gluten durum wheats in response to complaints that U.S. durum produces cooked spaghetti with insufficient firmness. Recent

releases of stronger gluten durums, such as the cultivar Vic, have been successful in overcoming the complaint. Farinograms of weak and strong durum wheat semolina, a commercial semolina, and a HRS wheat flour are shown in Fig. 10–36. Durum farinograms have a shorter arrival time and less stability than those for the HRS farinogram. However, Vic shows a stronger farinogram than 'Ward'. This measurement relates to the firmness scores, which are discussed in section 10–4.3.8. Although durum is not considered a bread wheat, Vic flour will produce a loaf of bread with greater volume than Ward flour.

10–4.3.2 Absorption

Water absorption of semolina is lower than that of HRS wheat flour. When durum is milled, some starch is damaged when reducing endosperm to flour, and the damaged starch readily absorbs water. In milling semolina, little starch damage occurs because the product is not reduced to such a small particle size; hence, there is less water absorption. Also, absorption is enhanced when more surface is exposed in a finely ground flour, and again the coarser particle size of semolina leads to less water absorption. In the production of pasta products that eventually are dried, low water absorption is desirable.

10–4.3.3 Semolina Color

Color is of prime importance in semolina, since the consumer generally expects yellow pasta products. The source of color in durum semolina is the xanthophylls, especially lutein. Semolina color is a highly heritable trait controlled primarily by additive gene effects (Johnston et al., 1983). Breeders have been successful in maintaining a bright yellow color in semolina milled from durum grown in the major durum producing area. Color can be estimated visually, such as with the Pekar test (AACC, 1983), in which semolina samples are placed side by side, smoothed with a flat steel plate, and the color observed. In most quality evaluation laboratories, color is measured directly with a reflectance colorimeter, or the pigment is extracted with water-saturated butanol and the pigment concentration is measured in a spectrophotometer. Johnston et al. (1980) compared the reflectance and extraction methods and found a high correlation.

While a good semolina color generally means that the extruded product will also have an acceptable color, there can be exceptions. Semolina from cultivars having high concentrations of the enzyme lipoxygenase can lose considerable color when the semolina and water are extruded into spaghetti and dried. An example is semolina from 'Golden Ball', which loses 51% of its color through processing (McDonald, 1979). Free linoleic acid plays an important role as the enzyme substrate (Matsuo et al., 1970). A possible reaction might be between lipoxygenase and the substrate linoleic acid to form linoleic acid hydroperoxides. These, in turn, may oxidize the pigments and destroy the color. Hsieh and McDonald

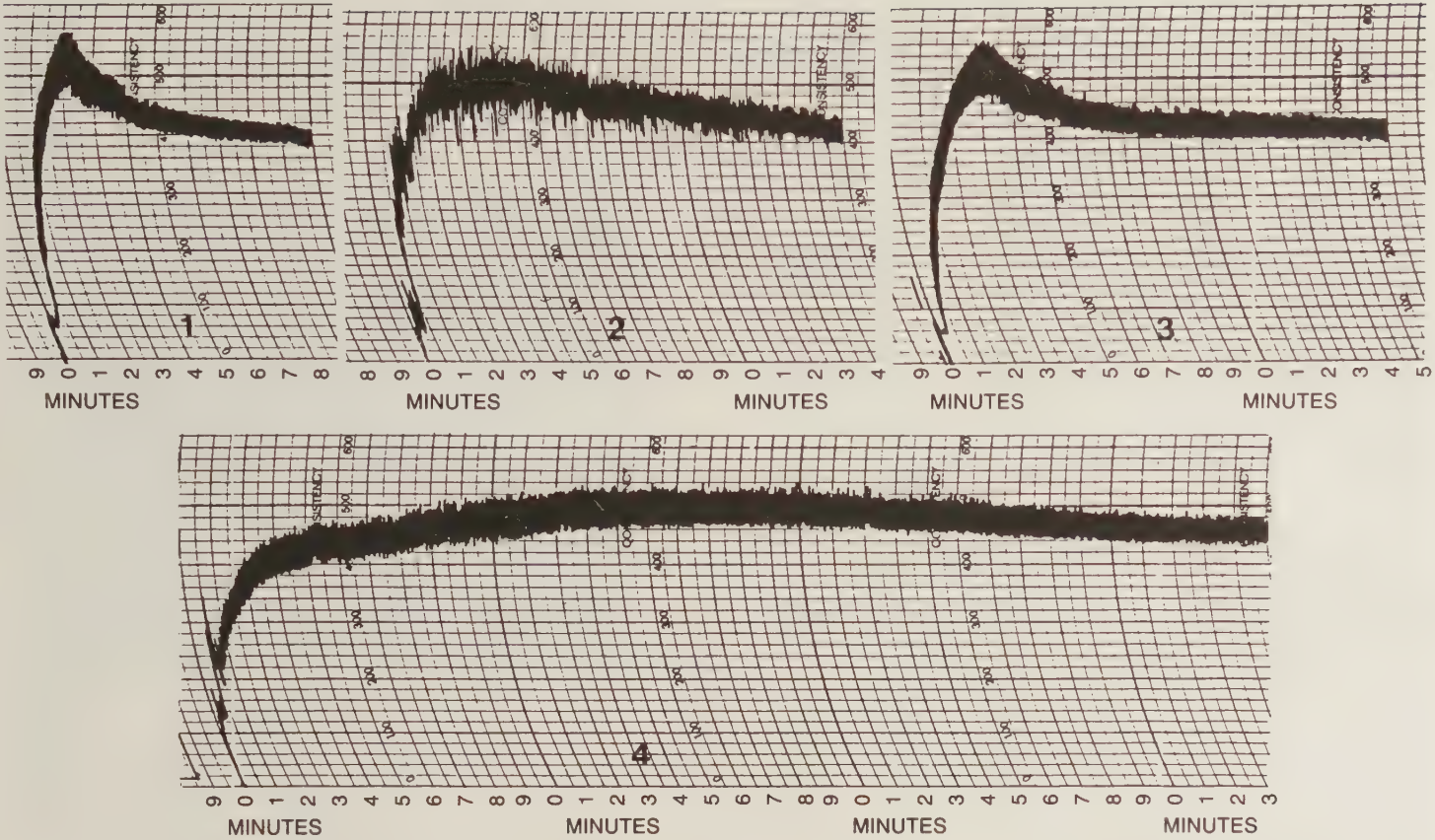

Fig. 10–36. Farinograms of (*1*) weak gluten semolina (Ward); (*2*) strong gluten semolina (Vic); (*3*) a commercial semolina; (*4*) HRS flour ('Len').

(1984) have identified from durum flour three lipoxygenase isoenzymes that promote the activity.

10-4.3.4 Amylase Activity

If α- and β-amylase enzymes are present in sufficient amounts, they can fragment the starch chains and ultimately affect the quality of the pasta. Normal durum wheat does not contain sufficient amylase to be a problem. However, if wet weather conditions exist during the durum harvest, sprouting can occur, and this may cause a major increase in α-amylase activity in the kernel. Amylase activity can be measured by a variety of methods (O'Connell et al., 1980; Kruger and Tipples, 1981; Mathewson et al., 1982; D'Appolonia et al., 1982), and the different methods can be satisfactorily related to each other. The amylograph and falling number methods are used most frequently. Both measure the effect of amylase on the gelatinization of starch.

The effect of sprouting on pasta quality has been studied (Dick et al., 1974; Donnelly, 1980; Kruger and Matsuo, 1982; and Matsuo et al., 1982). Sprouting at low levels has no effect on spaghetti quality. Opinions vary as to the effect of extensive sprouting, such as falling number values less than 100 s. At this level of sprouting, cooking loss and speck count may increase slightly, and spaghetti shelf stability may be decreased. Pasta manufacturers generally cite their own falling number specifications.

10-4.3.5 Speck Count

Specks can be bran pieces, particles from blackpoint, or other foreign material visible in semolina. A common method used is to count the specks in a 1-inch square with the aid of a magnifying glass. This is repeated three times, the numbers averaged, and converted to specks per 10 sq. inch. In addition to specks affecting the aesthetic quality of the pasta, bran pieces can weaken spaghetti strands.

10-4.3.6 Pasta Color

In the USA the majority of the durum pasta sold is in various forms and shapes of spaghetti, macaroni, and noodles. In the case of noodles, eggs are added and durum flour is used instead of semolina. A small segment of the market is made up of fortified pasta, and a variety of food materials have been added (Banasik and Dick, 1982).

Spaghetti is the major end product tested in durum quality evaluation. Yellow color in spaghetti or macaroni is considered very important. Similar to semolina, pasta color can be estimated visually but is generally measured with a reflectance colorimeter.

10-4.3.7 Cooked Weight

Cooking quality of spaghetti is also important. Optimum cooking time can be determined by pressing a strand of cooked spaghetti between

two glass plates. If cooking is not complete, a white thread of unhydrated material will be visible in the strand (Fig. 10–37). Cooked spaghetti should gain about three times its weight, and cooking loss should be only 5 to 6% at optimum cooking time.

10–4.3.8 Firmness or Tenderness

Good quality spaghetti should have the correct firmness or chewiness after cooking, and it should maintain this after some overcooking. The firmness of cooked spaghetti can be estimated by biting, but more precision is required in good quality evaluation, so instrumentation is often used. Walsh (1971) constructed a plastic tooth for the Instron Universal Testing Instrument and measured the work required to cut through a strand of cooked spaghetti. The method is still in use. Matsuo and Irvine (1969, 1971) designed and used an apparatus to simulate the bite test; it cuts cooked spaghetti, and the results are interpreted as a tenderness index.

Dexter et al. (1983) have used the Grain Research Laboratory bread compression tester to measure stickiness in spaghetti. They found that the quality of water for cooking and the procedure for drying spaghetti had a large influence on stickiness. Protein content was not related to stickiness.

There is a current interest in noodle testing, because of the importance of noodles throughout the world. Quality evaluation becomes complex, because quality requirements differ from country to country. Yellow noo-

Fig. 10–37. *Left*: Spaghetti strand, cooked for 6 min; note unhydrated center. *Right*: Spaghetti strand cooked for 12 min.

dles are preferred in the USA. Evaluation of cooking quality is important. Maximum cutting stress and resistance to compression of cooked noodles are two tests that related well to sensory evaluation of firmness and chewiness (Oh et al., 1983).

10–4.4 Prerequisites for Good Pasta-Processing Quality

For pasta products made from durum wheat, key factors that are essential include: (i) yellow color in the uncooked product; (ii) protein quality and quantity to provide strength, proper firmness, and stability to the cooked product; and (iii) low speck count. If noodles consumed in other parts of the world are considered, the picture is more complex, because the requirements vary considerably.

10–4.5 Milling Methods

Commercial milling systems have been described by Abercrombie (1980) and Nelstrop (1982). Good wheat cleaning procedures are important in durum milling. The presence of any grit in semolina is especially serious, because the grit may lodge in the die and cause splits and streaks in the extruded product. The time required to condition (temper) the wheat for milling varies with the vitreousness of the endosperm; water penetration is slower in highly vitreous kernels. Millers will often add a final portion of water to the previously tempered wheat just before milling to toughen the bran.

Typical mills use mostly break and sizing rolls and sometimes reduction rolls to reduce the particle size of by-products. Purifiers are used extensively to remove fine bran particles in the coarse ground material, because the bran would appear as undesirable specks in the semolina or the pasta product.

Quality laboratories associated with major durum breeding programs or major durum milling companies use experimental mills for evaluating the milling properties of durum wheat. Two batch methods have been described (AACC, 1983). A long flow system involves 10 breaks and seven purifiers; a short flow system uses four breaks, two reductions, and four purifiers. The Allis-Chalmers experimental mill system has been used (Dexter and Matsuo, 1978b; Matsuo and Dexter, 1980a, 1980b), and some durum mills are modifications of small experimental flour mills such as the Brabender Quadrumat Jr. (Fig. 10–38; Vasiljevic et al., 1977) and the Buhler mill (Fig. 10–39; Dexter et al., 1982; Sollberger, 1970; Black and Bushuk, 1967). Experimental purifiers are normally added to these mills to give a cleaner product (Vasiljevic et al., 1977; Black, 1966; Sibbitt et al., 1964).

In experimental milling, semolina yield is less than that produced by commercial mills, because fewer rolls are used. However, the semolinas are similar, so that quality evaluation is valid.

Fig. 10–38. Brabender Quadrumat Jr. converted to a durum experimental mill with small purifier beneath. The purifier uses a vacuum cleaner for its vacuum source.

10–4.6 Pasta-Processing Methods

10–4.6.1 Extrusion

Banasik (1981) and Walsh and Gilles (1974) have described commercial extrusion. Flow diagrams vary, depending upon the type of product to be formed, such as short goods (macaroni elbows) or long goods (spaghetti). Modern presses are equipped with a vacuum source to remove air bubbles that might form. Air bubbles affect the color and weaken the dried product. Many extruders are equipped with teflon-lined dies that give a smoother product, although sauce sticks to pasta better when the pasta is extruded through brass dies.

In experimental extrusion, attempts are made to duplicate the com-

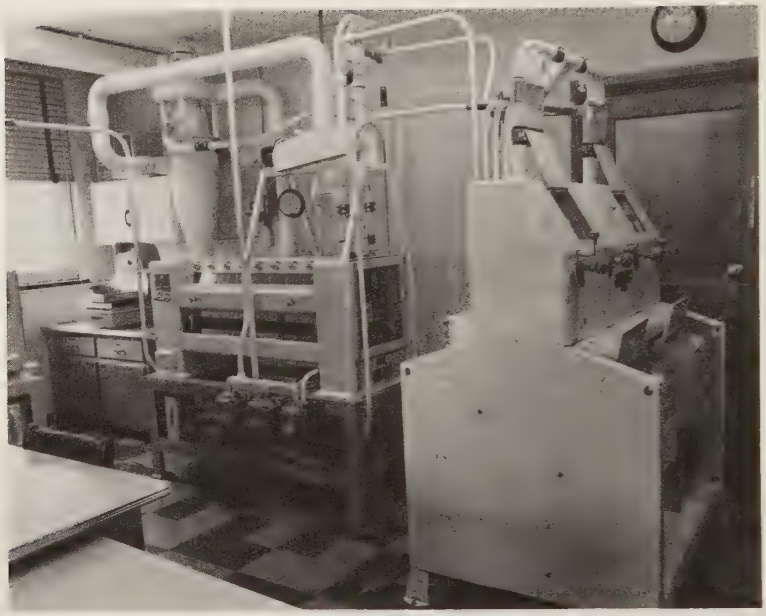

Fig. 10–39. Buhler mill converted to a durum experimental mill with purifier attached. This system also uses a second purifier, not visible.

mercial processes with small presses such as the De Maco extruder, which also mixes under vacuum and extrudes at a rate of 25 lb h^{-1}.

10–4.6.2 Drying

Drying is a critical step in pasta production. The moisture of the product must be slowly lowered from about 31 to 12% in a manner that will not create stresses when the pasta is dried. Excess stress would eventually cause checking and shattering. Commercial drying is often continuous, but generally in the first stages of drying the pasta is exposed to 95% relative humidity and a constant temperature of about 54 °C for a period of time. Then either the humidity is lowered or the pasta is moved to chambers of lower humidity and the same temperature. The entire process takes several hours, and if it is successful, the product will have good tensile strength and be free of mold growth or biological contamination. Excessively long drying times can promote mold or bacterial growth if microorganisms were present in the semolina, because temperatures during processing are not high enough to kill organisms. Drying cycles are designed especially to meet the needs of the product being dried.

In drying experimental samples for durum evaluation, the goals are the same. The extruded spaghetti is case hardened by allowing it to hang in the air about 30 min before beginning the drying cycle. Drying is almost always by the batch method, and a drying cabinet has been described by

Gilles et al. (1966). At the USDA Wheat Quality Laboratory, conventional drying is done at a constant temperature of 40 °C for 18 h. During this time the relative humidity is reduced from 95 to 60%.

The procedure used for drying experimental spaghetti at the Canadian Grain Research Laboratory has been described by Dexter et al. (1981). Temperature was maintained at 39 °C and the humidity lowered over a 28 h period.

High temperature drying (60 to 80 °C) has become popular. Advantages are reduced drying time, enhanced color, and improved cooking properties (Buhler-Miag, Inc., 1979; Dexter et al., 1981; Wyland and D'Appolonia, 1982; Ibrahim, 1982). Protein denaturation increased with the increase in drying temperature, which affected the nutritional value slightly by the destruction of lysine. Total starch was not affected by the drying temperature, and a small amount of starch gelatinization took place at high temperatures (Ibrahim, 1982). Temperatures above 80°C may adversely affect pasta color and probably will be avoided. More and more pasta drying, both commercial and experimental, is likely to be done at higher temperatures in the future. Also, microwave energy is now being used to dry some products. Microwave drying is said to speed the drying process and save valuable floor space.

10–4.7 Methods to Predict Functional Properties

Early generation screening tests on small quantities of grain to predict protein quantity, protein quality, pasta color, and pasta cooking quality are desired by durum plant breeders. Wheat protein quantity can be determined accurately on small samples by Kjeldahl or near-infrared analyses (NIRS). If the sample size is too small for milling, estimates of semolina protein can be made; these values will be about one percentage point less than wheat proteins.

Methods of estimating protein quality on small amounts have been described by Quick and Donnelly (1980), who used 6 g of ground whole meal for a sodium dodecyl sulfate (SDS) sedimentation test, and by Dick and Quick (1983), who developed a SDS microsedimentation test that used only 1 g of ground whole meal. Quick and Donnelly (1980) showed highly significant correlations between sedimentation values and mixogram scores, both obtained from corresponding semolina. Dick and Quick (1983) showed that good relationships existed when either the combined wheat protein and mixogram score or the combined wheat protein and microsedimentation score was related to cooked spaghetti firmness.

Early generation evaluation of semolina color is difficult unless enough of a sample is available for micromilling, such as in a modified Brabender Quadrumat Jr. Fairly good estimates of color can be obtained even if the semolina is specky. Color evaluation is non-destructive, so if the color readings are taken first, the sample is available for further analysis.

The mixograph is used routinely at the USDA Wheat Quality Lab (Fargo, ND) for evaluating gluten strength. Normally the 30-g mixograph

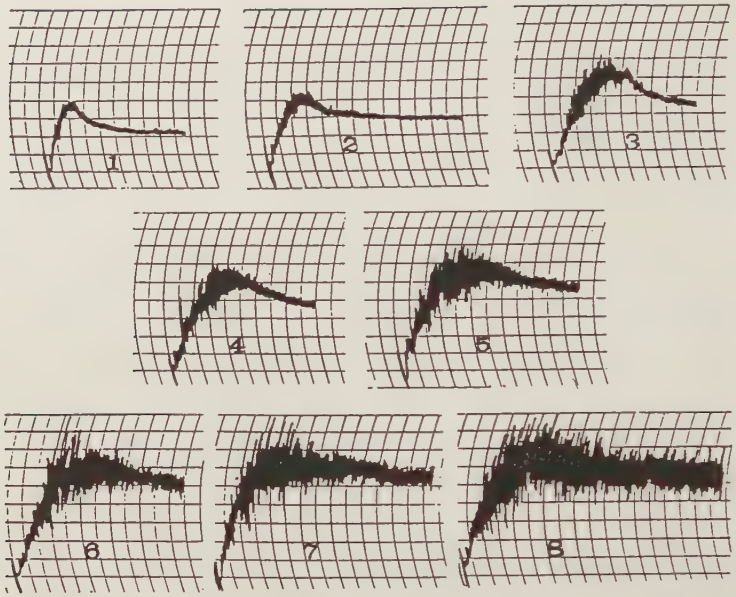

Fig. 10–40. Reference mixograms used in quick evaluation of gluten strength in durum selections.

is used if enough semolina is available, or the 10-g mixograph for smaller amounts. The resulting mixogram is a profile of gluten quality and correlates well with firmness (Dick and Quick, 1983). Figure 10–40 shows a range of gluten quality represented by several mixograms; durums with weak gluten would be similar to numbers 1 to 3. Since the mixograph is not standardized, mixograms from other instruments may not give the same pattern. However, relative changes among the mixograms should be similar.

The farinograph is not used to any extent in early generation testing because the amount of sample required is large (50 or 300 g). Also, the information obtained from farinograms is not as pertinent to predicting pasta quality as it is for predicting baking quality in bread wheats.

10–4.8 Contributions of Semolina Fractions to Pasta-Processing Properties

10–4.8.1 Protein and Protein Fractions

Durum proteins are acknowledged to be the most important fraction affecting pasta quality. The fractions comprising durum protein, such as

gliadins and glutenins, have received some attention. Chen and Bushuk (1970) used the classical Osborn fractionation procedure to compare protein fractions in durum, rye, triticale, and HRS wheat. Durum wheat endosperm was extremely low in water- and salt-soluble proteins (albumins and globulins) and extremely high in alcohol-soluble proteins (gliadins). Dexter and Matsuo (1977) used a similar procedure to fractionate two Canadian durum wheats at several protein levels and reported that albumins and globulins decreased significantly with increasing protein content. Their data related a high glutenin to gliadin ratio to superior cooking quality. This trend was also reported by Walsh and Gilles (1971) who used both Sephadex G-200 gel filtration and the Maes process (Mattern et al., 1968) on one HRS and seven durum cultivars, and by Wasik and Bushuk (1975), who used Sephadex G-150 gel filtration to isolate protein fractions from 15 durum wheat lines. In a later study on 30 durum wheat lines using the same fractionation methods, Dexter and Matsuo (1980) reported that an insoluble residue protein was the protein fraction most responsible for variations in gluten strength, farinograph properties, and spaghetti cooking quality.

Dexter and Matsuo (1978b) also fractionated gluten proteins from HRS and durum wheat by precipitation from 0.005 *M* lactic acid at various pH levels. As pH increased, the proportion of glutenins within each fraction decreased concomitantly with an increase in gliadins. In reconstitution studies a decrease in farinograph mixing time and pasta processing absorption accompanied this decrease in glutenins and increase in gliadins.

A strong relationship exists between the banding patterns of gliadin polypeptides separated by polyacrylamide gel electrophoresis (PAGE) and the gluten quality of the endosperm proteins of durum wheat (Damidauz et al., 1978, 1980; Kosmolak et al., 1980). The presence of gliadin band 45 and absence of band 42 is associated with strong gluten. PAGE of gliadin from the strong gluten cultivars Vic, Edmore, and Coulter have band 45 and no band 42 (Fig. 10–41). Several weak gluten cultivars have band 42 and no 45 (Khan, 1982). Both gliadin bands have similar amino acid composition and molecular weight of 45 000 daltons (Cottenet et al., 1983).

Joppa et al. (1978, 1983b) have produced a nearly complete set of durum aneuploids in which seven D-genome chromosomes were individually substituted for their respective A- or B-genome homologues. Also, chromosome 1B from Edmore, a strong gluten durum, was substituted into 'Langdon', a weak durum, using the Langdon 1D (1B) disomic-substitution line as the recurrent parent to produce Langdon (1B). Presence of the 1B chromosome in Langdon was further confirmed by

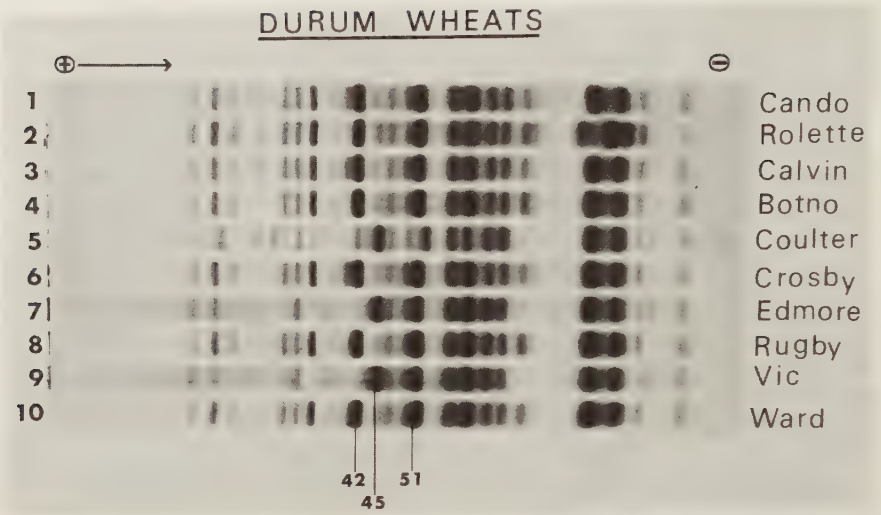

Fig. 10–41. Electrophoregram of strong and weak gluten durum wheats. Strong gluten cultivars show gliadin band 45, and weak gluten cultivars show gliadin band 42. Photo courtesy Khan, 1982.

PAGE, where band 45 was very strong. Semolinas from Langdon (1B), Langdon, and Edmore were analyzed for quality characteristics (Joppa et al., 1983a). In all analyses, Langdon (1B) and Edmore showed strong mixograms and high SDS sedimentation values, while Langdon was weak. Comparable results occurred in firmness tests of the cooked semolinas. Also, when bread was baked from Langdon (1B) or Edmore flour, loaf volumes were much greater than for bread baked from Langdon.

An interesting relationship exists between gliadin PAGE bands 42 and 45, mixogram and sedimentation tests, and glume color. In the Canadian plant breeding program it was found that buff-colored glumes were associated with weak gluten and PAGE band 42, while white glumes were associated with strong gluten and PAGE band 45 (Leisle et al., 1981). The possibilities of using these relationships in early generations for predicting gluten strength are exciting.

10–4.8.2 Carbohydrates

Carbohydrates are the major fraction found in semolina, yet their contribution to quality is secondary to that of protein. When Nelson (1983) added up to 10% durum starch to semolina, the color, cooked weight, and cooking loss of the spaghetti produced was not adversely affected. Firmness was reduced, but not significantly. Similar results were observed when chemically modified durum starches were added. Edmore, a strong gluten cultivar, was used in this study. The protein-diluting effects of added starch may have been more pronounced with weak gluten durums.

In the extrusion process, starch granules are surrounded by the pro-

tein matrix and align along the direction of flow of the dough through the extruder (Matsuo et al., 1978). Starch damage increases as semolina is processed, the greatest mechanical damage occurring when the dough is extruded (Lintas and D'Appolonia, 1973). Further modification of the starch takes place during drying by the action of amylolytic enzymes on the damaged starch. The increase in water-binding capacity, throughout the process, is related to the increase in damaged starch (Lintas and D'Appolonia, 1973).

Resmini and Pagani (1983) used electron microscopy to observe cooked pasta and found that cooking quality of pasta is determined by a physical competition between protein coagulation into a continuous network and starch swelling with spherulite scattering. If protein coagulation dominates, the starch granules are trapped in the network, promoting firmness. If the starch swells, and the protein lacks a continuous framework, the pasta may be soft and possibly sticky.

10-4.8.3 Lipids

Hexane-soluble or free lipids make up $< 1\%$ of the semolina weight, and most of the lipids become bound after extrusion. The nonpolar, bound lipids may just be enveloped in a protein matrix, or they may be chemically bound to protein during the mixing process. Dahle and Muenchow (1968) extracted spaghetti strands with various solvents and cooked the extracted spaghetti. Removal of lipids increased stickiness, and removal of lipids and protein increased stickiness, softness, and pastiness. They concluded that protein played a more important role than lipids in cooking quality. When Lin et al. (1974) extracted durum semolina with petroleum ether, water absorption increased, and yellow color was lost in spaghetti. Addition of 0.6% nonpolar lipids to defatted semolina restored spaghetti color. Nonpolar lipids and monogalactosyl diglyceride slightly increased water absorption of untreated semolina and the firmness of the spaghetti, while digalactosyl diglycerides and phospholipids decreased those factors. Lipids had little effect on the cooking quality of spaghetti.

REFERENCES

Abercrombie, E. 1980. Durum milling. p. 3808–3813. *In* Assoc. of Operative Millers-Bull. March, April, May, June. Kansas City, MO.

AACC. 1983. Approved methods of the AACC. 8th ed. Method 26–30, approved April 1961; Method 14–10, reviewed October 1982. American Association of Cereal Chemists, St. Paul.

Banasik, O.J. 1981. Pasta processing. Cereal Foods World 26:166–169.

----, and J.W. Dick. 1982. Extruded products from durum wheat. Cereal Foods World 27:553–557.

Barmore, M.A. 1959. The Western Wheat Quality Laboratory. Cereal Sci. Today 4:235–238.

Black, H.C. 1966. Laboratory purifier for durum semolina. Cereal Sci. Today 11:533–542.

----, and W. Bushuk. 1967. Modification of the Buhler laboratory mill for milling semolina. Cereal Sci. Today 12:164–168.

Bloksma, A.H. 1971. Rheology and chemistry of dough. p. 523–584. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Bode, C.E. 1959. The Soft Wheat Quality Laboratory. Cereal Sci. Today 4:259–263, 280.

Brabender, C.W. 1965. Physical dough testing: past, present and future. Cereal Sci. Today 10:291–304.

Bruinsma, B.L., and K.F. Finney. 1981. Functional (breadmaking) properties of a new dry yeast. Cereal Chem. 58(5):477–480.

----, and G.L. Rubenthaler. 1978. Estimation of lysine and texture in cereals by NIR. p. X-BR-1-X-BR-16. Proc. 8th Technicon Int. Congr., London, U.K. 12–14 Dec. 1978. Technicon Instruments Co., Ltd., Basingstoke, U.K.

Buhler-Miag, Inc. January 1979. "High temperature" drying of pasta products. Macaroni J. 60:30, 32.

Chen, C.H., and W. Bushuk. 1970. Nature of proteins in *Triticale* and its parental species. I. Solubility characteristics and amino acid composition of endosperm proteins. Can. J. Plant Sci. 50:9–14.

Chung, O.K., Y. Pomeranz, and K.F. Finney. 1978. Wheat flour lipids in breadmaking. Cereal Chem. 55(5):598–618.

----, ----, and ----. 1982. Relation of polar lipid content to mixing requirement and loaf volume potential of hard red winter wheat flour. Cereal Chem. 59(1):14–20

Clements, R.L., and Donelson, J.R. 1981. Functionality of specific lipids in cookies. Cereal Chem. 58:204–206.

----, and ----. 1982a. Role of free flour lipids in batter expansion in layer cakes. I. Effects of "aging." Cereal Chem. 59:121–124.

----, and ----. 1982b. Role of free flour lipids in batter expansion in layer cakes. II. Effects of heating. Cereal Chem. 59:125–128.

Cottenet, M., J. Autran, and P. Joudrier. 1983. Isolation and characterization of gamma-gliadins 45 and 42 compounds associated to viscoelastic characteristics of the gluten of durum wheat. C. R. Hebd. Seances Acad. Sci. Ser. D 297:149–154.

Dahle, L.K., and H.L. Muenchow. 1968. Some effects of solvent extraction on cooking characteristics of spaghetti. Cereal Chem. 45:464–468.

Damidaux, R., J.C. Autran, P. Grignac, and P. Feillet. 1978. Mise en évidence de relations applicables en selection entre l'électrophoregramme des gliadins et les propriétés visco-élastiques du gluten de *Triticum durum* Desf. C. R. Hebd. Seances Acad. Sci. Ser. D 287:701–704.

----, ----, ----, and ----. 1980. Déterminisme génétique des constituants gliadines de *Triticum durum* Desf. associés à la qualité culinaire intrinsèque des variétés. C. R. Hebd. Seances Acad. Sci. Ser. D 291:585–588.

D'Appolonia, B.L., K.A. Gilles, E.M. Osman, and Y. Pomeranz. 1971. Carbohydrates. p. 301–392. *In.* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

----, L.A. MacArthur, W. Pisesookbunterng, and C.F. Ciacco. 1982. Comparison of the grain amylase analyzer with the amylograph and falling number methods. Cereal Chem. 59:254–257.

Dexter, J.E., H.C. Black, and R.R. Matsuo. 1982. An improved method for milling semolina in the Buhler laboratory mill and a comparison to the Allis-Chalmers laboratory mill. Can. Inst. Food Sci. Technol. J. 15:225–228.

----, R.H. Kilborn, B.C. Morgan, and R.R. Matsuo. 1983. Grain Rsearch Laboratory compression tester: Instrumental measurement of cooked spaghetti stickiness. Cereal Chem. 60:139–142.

----, and R.R. Matsuo. 1977. Influence of protein content on some durum wheat quality parameters. Can. J. Plant Sci. 57:717–727.

----, and ----. 1978a. Effect of semolina extraction rate on semolina characteristics and spaghetti quality. Cereal Chem. 55:841–852.

----, and ----. 1978b. The effect of gluten protein fractions on pasta dough rheology and spaghetti-making quality. Cereal Chem. 55:44–57.

----, and ----. 1980. Relationship between durum wheat protein properties and pasta dough rheology and spaghetti cooking quality. J. Agric. Food Chem. 28:899–902.

----, and ----. 1981. Effect of starchy kernels, immaturity, and shrunken kernels on durum wheat quality. Cereal Chem. 58:395–400.

----, and ----, B.C. Morgan. 1981. High temperature drying: Effect on spaghetti properties. J. Food Sci. 46:1741–1746.

Dick, J.W., and J.S. Quick. 1983. A modified screening test for rapid estimation of gluten strength in early-generation durum wheat breeding lines. Cereal Chem. 60:315–318.

----, D.E. Walsh, and K.A. Gilles. 1974. The effect of field sprouting on the quality of durum wheat. Cereal Chem. 51:180–188.

Donnelly, B.J. Nov. 1980. Effect of sprout damage on durum wheat quality. Macaroni J. 62:8–10, 14.

Faridi, H.A., and Finney, P.L. 1980. Technical and nutritional aspects of Iranian breads. Baker's Dig. 54(5):14, 19–20, 22.

----, and Rubenthaler, G.L. 1983a. Experimental baking techniques for evaluating Pacific Northwest wheats in North African breads. Cereal Chem. 60:74–79.

----, and ----. 1983b. Ancient breads and a new science: Understanding flat breads. Cereal Foods World 28:627–629.

Finney, K.F. 1943. Fractionating and reconstituting techniques as tools in wheat flour research. Cereal Chem. 20:381–396.

----. 1945. Methods of estimating and the effect of variety and protein level on the baking absorption of flour. Cereal Chem. 22:149–158.

----. 1954. Contributions of the Hard Winter Wheat Quality Laboratory to wheat quality research. Trans. Am. Assoc. Cereal Chem. 12:127–142.

----. 1964. Quality evaluation of early-generation wheat progenies. p. 74–83. *In* Rep. of 2nd Natl. Conf. on Wheat Utilization Research, Peoria, IL. 28–30 Oct. 1963. USDA Unnumbered processed report. Peoria, IL.

----. 1971. Fractionating and reconstituting techniques to relate functional (breadmaking) to biochemical properties of wheat flour components. Cereal Sci. Today 16(10):342–356.

----. 1978a. Genetically high protein hard winter wheat. Baker's Dig. 52(3):32–35.

----. 1978b. Contribution of individual chemical constituents to the functional (breadmaking) properties of wheat. p. 267–288. *In* H.O. Hultin and M. Milner (ed.) Postharvest biology and biotechnology. Food and Nutrition Press, Westport, CT.

----. 1979. Wheat proteins: What they do. p. 50–61. *In* Proc. Wheat Protein Conf., Manhattan, KS. 16–17 Oct. 1978. USDA-AR Manual ARM-9. Peoria, IL.

----. 1984. An optimized, straight-dough, bread-making method after 44 years. Cereal Chem. 61(1):20–27.

----. 1985. Experimental breadmaking studies, functional (breadmaking) properties, and related gluten protein fractions. Cereal Foods World 30(11):794–801.

----, and M.A. Barmore. 1943. Yeast variability in wheat variety test baking. Cereal Chem. 20:194–200.

----, and ----. 1945a. Varietal responses to certain baking ingredients essential in evaluating the protein quality of hard winter wheats. Cereal Chem. 22:225–243.

----, and ----. 1945b. Optimum vs. fixed mixing time at various potassium bromate levels in experimental bread making. Cereal Chem. 22:244–254.

----, and ----. 1948. Loaf volume and protein content of hard winter and spring wheats. Cereal Chem. 25:291–312.

----, and Bolte, L.C. 1985. Experimental micromilling: Reduction of tempering time of wheat from 18-24 hours to 30 minutes. Cereal Chem. 62(6):454–458.

----, and H.C. Fryer. 1958. Effect on loaf volume of high temperatures during the fruiting period of wheat. Agron. J. 50:28–34.

----, E.G. Heyne, M.D. Shogren, L.C. Bolte, and Y. Pomeranz. 1985. Functional properties of some European wheats when grown in Europe and Kansas. Cereal Chem. 62:83–88.

----, B.L. Jones, and M.D. Shogren. 1982. Functional (breadmaking) properties of wheat protein fractions obtained by ultracentrifugation. Cereal Chem. 59:449–453.

----, V.H. Morris, and W.T. Yamazaki. 1950. Micro versus macro cookie baking procedures for evaluating the cookie quality of wheat varieties. Cereal Chem. 27:42–49.

----, and M.D. Shogren. 1972. A ten-gram mixograph for determining and predicting functional properties of wheat flours. Baker's Dig. 46(2):32–35, 38–42, 77.

----, and W.T. Yamazaki. 1946. A micro-milling technique using the Hobart grinder. Cereal Chem. 23:484–492.

----, and ----. 1967. Quality of hard, soft, and durum wheats. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:471–503.

Finney, P.L., C.D. Magoffin, R.C. Hoseney, and K.F. Finney. 1976. Short-time baking systems. I. Interdependence of yeast concentration, fermentation time, proof time, and oxidation requirement. Cereal Chem. 53:126–134.

Fortmann, K.L., and R.R. Joiner. 1971. Wheat pigments and flour color. p. 493–522. *In.* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Gaines, C.S., and J.R. Donelson. 1981. Contribution of chlorinated flour fractions to cake crumb stickiness. Cereal Chem. 59:378–380.

Gilles, K.A., L.D. Sibbitt, and W.C. Shuey. 1966. Automatic laboratory dryer for macaroni products. Cereal Sci. Today 11:322–324.

Goforth, D.R., and K.F. Finney. 1976. Communication to the Editor: Separation of glutenin from gliadin by ultracentrifugation. Cereal Chem. 53(4):608–612. (Erratum 53(5):820.)

Hanson, Haldore, N.E. Borlaug, and R.G. Anderson. 1982. Wheat in the third world. Westview Press, Boulder, CO.

Heyne, E.G., and G.S. Smith. 1967. Wheat breeding. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:269–306.

Hoseney, R.C., and K.F. Finney. 1971. Functional (breadmaking) and biochemical properties of wheat flour components. XI. A review. Baker's Dig. 45(4):30–36, 39–40, 64–67.

----, ----, and Y. Pomeranz. 1970. Functional (breadmaking) and biochemical properties of wheat flour components. VI. Gliadin-lipid-glutenin interaction in wheat gluten. Cereal Chem. 47:135–140.

----, ----, M.D. Shogren, and Y. Pomeranz. 1969. Functional (breadmaking) and biochemical properties of wheat flour components. II. Role of water solubles. Cereal Chem. 46:117–125.

Hsieh, C.C., and C.E. McDonald. 1984. Isolation of lipoxygenase isoenzymes from flour of durum wheat endosperm. Cereal Chem. 61:392–398.

Ibrahim, R.H.R. 1982. High temperature drying of pasta: Effect on quality and biochemical components. Ph.D. diss. North Dakota State Univ., Fargo (Diss. Abstr. 82–25530).

Irvine, G.N. 1971. Durum wheat and paste products. p. 777–796. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Jeffers, H.C., and G.L. Rubenthaler. 1977. Effect of roll temperature on flour yield with the Brabender Quadrumat experimental mill. Cereal Chem. 54:1018–1025.

Johnston, R.A., J.S. Quick, and B.J. Donnelly. 1980. Note on comparison of pigment extraction and reflectance colorimeter methods for evaluating semolina color. Cereal Chem. 57:447–448.

----, ----, and J.J. Hammond. 1983. Inheritance of semolina color in six durum wheat crosses. Crop Sci. 23:607–610.

Jones, B.L., K.F. Finney, and G.L. Lookhart. 1983. Physical and biochemical properties of wheat protein fractions obtained by ultracentrifugation. Cereal Chem. 60:276–280.

Joppa, L.R., J.A. Bietz, and N.D. Williams. 1978. The aneuploids of durum wheat: D-genome addition and substitution lines. p. 420–426. *In* S. Ramanujam (ed.) Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. 23–28 Feb. 1978. Indian Society of Genetics and Plant Breeding, Indian Agricultural Research Institute, New Delhi.

----, C. Josephides, and V.L. Youngs. 1983a. Chromosomal location of genes affecting quality in durum wheat. p. 297–301. *In* S. Sakamoto (ed.) Proc. 6th Int. Wheat Genet. Symp., Kyoto, Japan. 28 November–3 December. Plant Germ-Plasm Institute, Kyoto University, Kyoto.

----, K. Khan, and N.D. Williams. 1983b. Chromosomal location of genes for gliadin polypeptides in durum wheat *Triticum turgidum* L. Theor. Appl. Genet. 64:289–293.

Kasarda, D.D., C.C. Nimmo, and G.O. Kohler. 1971. Proteins and the amino acid composition of wheat fractions. p. 227–299. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Kemp, J.G., A.G.O. Whiteside, D.C. MacDonald, and H. Miller. 1961. Ottawa micro flour mill. Cereal Chem. 38:50–59.

Khan, K. 1982. Polyacrylamide gel electrophoresis of wheat gluten proteins. Baker's Dig. 56(5):14–19.

Kissell, L.T., J.R. Donelson, and R.L. Clements. 1979. Functionality in white layer cake of lipids from untreated and chlorinated patent flours. I. Effects of free lipids. Cereal Chem. 56:11–14.

----, and W.T. Yamazaki. 1979. Cake-baking dynamics: Relation of flour-chlorination rate to batter expansion and layer volume. Cereal Chem. 56:324–327.

Kosmolak, F.G., J.E. Dexter, R.R. Matsuo, D. Leisle, and B.A. Marchylo. 1980. A relationship between durum wheat quality and gliadin electrophoregrams. Can. J. Plant Sci. 60:427–432.

Kruger, J.E., and R.R. Matsuo. 1982. Comparison of alpha-amylase and simple sugar levels in sound and germinated durum wheat pasta processing and spaghetti cooking. Cereal Chem. 59:26–31.

----, and K.H. Tipples. 1981. Modified procedure for use of Perkin-Elmer Model 191 Grain Amylase Analyzer in determining low levels of alpha-amylase in wheats and flours. Cereal Chem. 58:271–274.

Leisle, D., G. Kosmolak, and M. Kovacs. 1981. Association of glume color with gluten strength and gliadin proteins in durum wheat. Can. J. Plant Sci. 61:149–151.

Lin, M.J.Y., B.L. D'Appolonia, and V.L. Youngs. 1974. Hard red spring and durum wheat polar lipids. II. Effect on quality of bread and pasta products. Cereal Chem. 51:34–45.

Lintas, C., and B.L. D'Appolonia. 1973. Effect of spaghetti processing on semolina carbohydrates. Cereal Chem. 50:563–570.

MacMasters, M.M., J.J.C. Hinton, and D. Bradbury. 1971. Microscopic structure and composition of the wheat kernel. p. 51–113. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Magoffin, C.D., P.L. Finney, and K.F. Finney. 1977. Short-time baking systems. II. A sugar-free formula for conventional and high-protein breads. Cereal Chem. 54:760–769.

Mathewson, P.R., C.H. Fahrenholz, G.D. Booth, Y. Pomeranz, and B.S. Miller. 1982. Results of collaborative testing using a simplified, rapid colorimetric alpha-amylase assay for evaluation of sprouted wheat. Cereal Chem. 59:108–112.

Matsuo, R.R., J.W. Bradley, and G.N. Irvine. 1970. Studies on pigment destruction during spaghetti processing. Cereal Chem. 47:1–5.

----, and J.E. Dexter. 1980a. Relationship between some durum wheat physical characteristics and semolina milling properties. Can. J. Plant Sci. 60:49–53.

----, and ----. 1980b. Comparison of experimentally milled durum wheat semolina to semolina produced by some Canadian commercial mills. Cereal Chem. 57:117–122.

----, ----, and B.L. Dronzek. 1978. Scanning electron microscopy study of spaghetti processing. Cereal Chem. 55:744–753.

----, ----, and A.W. MacGregor. 1982. Effect of sprout damage on durum wheat and spaghetti quality. Cereal Chem. 59:468–472.

----, and G.N. Irvine. 1969. Spaghetti tenderness testing apparatus. Cereal Chem. 46:1–6.

----, and ----. 1971. Note on an improved apparatus for testing spaghetti tenderness. Cereal Chem. 48:554–558.

Mattern, P.J., A. Salem, and G.H. Volkmer. 1968. Modification of the Maes continuous-extraction process for fractionation of hard red winter wheat flour proteins. Cereal Chem. 45:319–328.

McDonald, C.E. 1979. Lipoxygenase and lutein bleaching activity of durum wheat semolina. Cereal Chem. 56:84–89.

Miller, B.S., Bette Hays, and J.A. Johnson. 1956. Correlation of farinograph, mixograph, sedimentation, and baking data for hard red winter wheat flour samples varying widely in quality. Cereal Chem. 33:277–290.

----, and J.A. Johnson. 1954. A review of methods for determining the quality of wheat and flour for breadmaking. Kans. Agric. Exp. Stn. Tech. Bull. 76.

Miller, Dwight L. 1974. Industrial uses of wheat and flour. p. 398–411. *In* George E. Inglett (ed.) Wheat: Production and utilization. AVI Publications Co., Westport, CT.

Monsivais, M., R.C. Hoseney, and K.F. Finney. 1983. The Pelshenke test and its value in estimating bread-making properties of hard winter wheats. Cereal Chem. 60:51–55.

Morris, Rosalind. 1975–1984. Chromosomal locations of genes for wheat characters compiled from the literature. p. i. *In* Annu. wheat newsl., Vol. 21–30. E.G. Heyne and A.B. Campbell (ed.) (1975–1981), E.G. Heyne and J.S. Noll (ed.) (1982), Kansas State Univ., Manhattan, and J.S. Quick and J.S. Noll (ed.) (1983–1984), Colorado State Univ., Fort Collins.

Nagao, S., S. Imai, T. Sato, Y. Kaneko, and H. Otsubo. 1976. Quality characteristics of soft wheat and their use in Japan. I. Methods of assessing wheat suitability for Japanese products. Cereal Chem. 53:988–997.

----, S. Ishibashi, S. Imai, T. Sato, T. Kanbe, Y. Kaneko, and H. Otsubo. 1977. Quality characteristics of soft wheats and their utilization in Japan. II. Evaluation of wheats from the United States, Australia, France, and Japan. Cereal Chem. 54:198–204.

Nelson, J. 1983. Modification of starch and its effect on pasta quality. Ph.D. diss. North Dakota State Univ., Fargo (Diss. Abstr. 83-08387).

Nelstrop, P.C. Nov. 1982. A closer look at semolina milling. Milling 154:16–18, 20, 22, 25–26.

Noguchi, G. 1978. Baking quality of Pacific Northwest soft white wheats in Japanese sponge cake. M.S. thesis. Washington State Univ., Pullman, WA.

O'Connell, B.T., G.L. Rubenthaler, and N.L. Murbach. 1980. Evaluation of a nephelometric method for determining cereal alpha-amylase. Cereal Chem. 57:411–415.

Oh, N.H., P.A. Seib, C.W. Deyoe, and A.B. Ward. 1983. Noodles. I. Measuring the textural characteristics of cooked noodles. Cereal Chem. 60:433–438.

Olcott, H.S., and D.K. Mecham. 1947. Characterization of wheat gluten. I. Protein-lipid complex formation during doughing of flours. Lipoprotein nature of the glutenin fraction. Cereal Chem. 24:407–414.

Pomeranz, Y. 1971. Composition and functionality of wheat-flour components. p. 585–674. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Quick, J.S., and B.J. Donnelly. 1980. A rapid test for estimating durum wheat gluten quality. Crop Sci. 20:816–818.

Reed, G., and J.A. Thorn. 1971. Enzymes. p. 453–491. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Reitz, L.P. 1967. World distribution and importance of wheat. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:1–18.

Resmini, P., and M.A. Pagani. 1983. Ultrastructure studies of pasta. A review. Food Microstruct. 2:1–12, 98.

Rubenthaler, G.L., and H. Faridi. 1981. Breads produced from Pacific Northwest soft white wheat. I. Five international breads. Baker's Dig. 55(6):19–22.

Schruben, L.W., and E.F. Seeborg. 1967. Marketing wheat. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:505–549.

Seeborg, E.F. 1951. Evaluation of wheat milling characteristics by laboratory methods. Trans. Am. Assoc. Cereal Chem. 9:25–30.

Shellenberger, J.A., Y. Pomeranz, K.F. Finney, and A.B. Ward. 1970. Chemical, rheological and breadmaking characteristics of selected varieties of various wheat classes. Baker's Dig. 44(5):27–31, 34–35.

----, and A.B. Ward. 1967. Experimental milling. *In* K.S. Quisenberry and L.P. Reitz (ed.) Wheat and wheat improvement. 1st ed. Agronomy 13:445–469.

Shogren, M.D., and K.F. Finney. 1974. A mixture of ascorbic acid and potassium bromate quickly optimize loaf volume. Cereal Sci. Today 19(9):397. (Abstr.)

----, and ----. 1984. Bread-making test for 10 g of flour. Cereal Chem. 61:418–423.

----, ----, L.C. Bolte, and R.C. Hoseney. 1963a. A modified alveograph method for hard winter wheat flour. Agron. J. 55:19–21.

----, ----, ----, and ----. 1963b. Correlations of certain properties of the alveogram with important hard winter wheat quality characteristics. Agron. J. 55:21–24.

Shoup, N.H., K.L. Pell, E.F. Seeborg, and M.A. Barmore. 1957. A new micro mill for preliminary milling-quality tests of wheat. Cereal Chem. 34:296–298.

Sibbitt, L.D., W.C. Shuey, and K.A. Gilles. 1964. A small laboratory purifier. Cereal Sci. Today 9:436–439.

Sollars, W.F., and F.F. Barrett. 1964. Soft wheat flour evaluation at the Western Wheat Quality Laboratory. Baker's Dig. 38:34–39.

Sollberger, H. 1970. Lab grinding test for durum semolina. Northwest. Miller 277:8–14.

USDA. 1977. The official United States standards for grain. USDA Fed. Grain Insp. Serv., U.S. Government Printing Office, Washington, DC.

----. 1982. Agricultural statistics. U.S. Government Printing Office, Washington, DC.

Vasiljevic, S., O.J. Banasik, and W.C. Shuey. 1977. A micro unit for producing durum semolina. Cereal Chem. 54:397–404.

Walsh, D.E. 1971. Measuring spaghetti firmness. Cereal Sci. Today 16:202–205.

----, and K.A. Gilles. 1971. The influence of protein composition on spaghetti quality. Cereal Chem. 48:544–554.

----, and ----. 1974. Macaroni products. p. 333–354. *In.* D.E. Inglett (ed.) Wheat: Production and utilization. AVI Publishing Co., Westport, CT.

Wasik, R.J., and W. Bushuk. 1975. Relation between molecular-weight distribution of endosperm proteins and spaghetti-making quality of wheats. Cereal Chem. 52:322–328.

Williams, P.C. 1975. Application of near infrared reflectance spectroscopy to analysis of cereal grains and oilseeds. Cereal Chem. 52:561–576.

----. 1979. Screening wheat for protein and hardness by near infrared reflectance spectroscopy. Cereal Chem. 56:169–172.

----, K.H. Norris, and W.S. Zarowski. 1982. Influence of temperature on estimation of protein and moisture in wheat by near-infrared reflectance. Cereal Chem. 59:473–477.

Wyland, A.R., and B.L. D'Appolonia. 1982. Influence of drying temperature and farina blending on spaghetti quality. Cereal Chem. 59:199–201.

Yamazaki, W.T. 1953. An alkaline water retention capacity test for the evaluation of cookie baking potentialities of soft winter wheat flours. Cereal Chem. 30:242–246.

----. 1954. Interrelations among bread dough absorption, cookie diameter, protein content, and alkaline water retention capacity of soft winter wheat flours. Cereal Chem. 31:135–142.

----. 1970. AACC Technical Committee Report: White layer cake test. Cereal Sci. Today 15:262–264, 266–268.

----, and L.C. Andrews. 1982a. Experimental milling of soft wheat cultivars and breeding lines. Cereal Chem. 59:41–45.

----, and ----. 1982b. Small-scale milling to estimate the milling quality of soft wheat cultivars and breeding lines. Cereal Chem. 59:270–272.

----, and L.W. Briggle. 1969. Components of test weight in soft wheat. Crop Sci. 9:457–460.

----, and D.H. Donelson. 1972a. The relationship between flour particle size and cake-volume potential among eastern soft wheats. Cereal Chem. 49:649–653.

----, and J.R. Donelson. 1972b. Evaluating soft wheat quality in early generation progenies. Crop Sci. 12:374–375.

----, and ----. 1976. Effects of interactions among flour lipids, other flour fractions, and water on cookie quality. Cereal Chem. 53:998–1005.

----, and ----. 1983. Kernel hardness of some U.S. wheats. Cereal Chem. 60:344–350.

----, ----, and W.F. Kwolek. 1977. Effects of flour fraction composition on cookie diameter. Cereal Chem. 54:352–360.

----, and L.T. Kissell. 1978. Cake flour and baking research: A review. Cereal Foods World 23:114–119.

----, and D.D. Lord. 1971. Soft wheat products. p. 743–776. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

Ziegler, E., and E.N. Greer. 1971. Principles of milling. p. 115–199. *In* Y. Pomeranz (ed.) Wheat chemistry and technology. American Association of Cereal Chemists, St. Paul.

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